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Prey Selection by Young Lemon Sharks (Negaprion brevirostris) at Chandeleur Island Nursery Habitats with a Comparison to Three Other Co-Occurring Shark Species

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Dedication

I dedicate this manuscript to my late grandfather Thomas Charbonneau. He was a loving and giving man who was always there for his family and inspired me to never give up on my dreams. Thanks Grandpa for your spirit and wisdom which I carry with me every day.

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Abstract

The Chandeleur Islands (Louisiana) contain nursery habitats for lemon sharks that provide abundant prey and protection from predation. Other local shark species (Atlantic sharpnose, bull, and blacktip sharks) co-occur with lemon sharks in the same region, including the nearby Biloxi Marshes. To better assess how lemon sharks use these nursery habitats, I measured diet and prey availability of young of the year and juvenile lemon sharks from 2009 to 2010. Young lemon sharks at the Chandeleur Islands have a relatively reduced diet breadth in comparison to those from nurseries in Bimini (Bahamas) and the Florida Keys. At the Chandeleur Islands, young lemon sharks appear to be opportunistically feeding on the most abundant prey items, resulting in high prey abundance and low diversity in their diet. Opportunistic feeding by young lemon sharks suggests minimal dietary overlap with other local shark species, resulting in minimal competition for resources.

Keywords: lemon shark, Chandeleur Islands, nursery habitat, Biloxi Marshes, sharks

Introduction

Many shark species are large and their size influences feeding and reproductive ecology (Branstetter, 1990). Most importantly, large size assists sharks in being effective predators. Larger fishes, in general, possess sustainable pursuit swimming speeds, long distance cruising abilities, larger gape sizes, and active defense mechanisms (Helfman et al., 1997). Sharks possess k-selected life history traits such as slow growth, late maturity, low fecundity, low natural mortality, and long life spans (Feldheim et al., 2001a; Gruber et al., 2001; Freitas et al., 2006). Females give birth to relatively few young after long gestation times resulting in increased maternal investment and significantly low recruitment rates (Feldheim et al., 2001). Successful recruitment rates are heavily dependent on low natural mortality and the presence of essential nursery grounds (Castro, 1993; Feldheim et al., 2001b; 2002). Females of large shark species travel long distances to these critical nursery habitats to lay eggs or give birth to live young (Castro, 1993; Feldheim et al., 2001b; 2002; Barker et al., 2005). Without their large size and swimming abilities, such necessary migrations would be impossible.

Shark nursery areas typically occur in shallow coastal waters including bays, estuaries, and reef lagoons (Dibattista et al., 2005; Freitas et al., 2006; DeAngelis et al., 2008). All age classes of sharks of multiple species can co-occur in these valuable nursery habitats for different reasons. The social interactions of neonates, juveniles, and adults of multiple species within these critical nursery habitats are a delicate balance of habitat partitioning and food availability. For example, the Mississippi Sound and its associated barrier islands along with the lower reaches of Mobile Bay have all been identified as important nursery habitats for multiple shark species such as Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), blacktip sharks (*Carcharhinus limbatus*), and finetooth sharks (*C. isodon*; Parsons and Hoffmayer, 2007).

Similar use of nursery habitats by multiple shark species has been observed in South Carolina (Castro, 1993). The north-central Gulf of Mexico as a whole is an important ecosystem for bull sharks (*C. leucas*), scalloped hammerhead sharks (*Sphyrna lewini*), bonnethead sharks (*S. tiburo*), spinner sharks (*C. brevipinna*), blacknose sharks (*C. acronotus*), and sandbar sharks (*C. plumbeus*; Parsons and Hoffmayer, 2007). While little is known how multiple shark species use these nursery habitats concurrently, habitat partitioning by juvenile *N. brevirostris* and *C. limbatus* has been recorded within nursery habitats at Fish Bay in the U.S. Virgin Islands (DeAngelis et al., 2008). Unlike other species, young *N. brevirostris* and *C. limbatus* remained in shallow depths primarily as a means of avoiding predators (DeAngelis et al., 2008). The interactions among shark species that determine shark assemblage structure in nursery habitats are incredibly complex. Inter- and intraspecific interactions among shark species (e.g., predation, cannibalism, etc.) influence where different species can survive. Sharks choose nursery habitats based on whether the physical conditions are conducive to growth and development, whether appropriate prey items are nearby, and whether there are reduced biological interactions stemming from predation and competition (Parsons and Hoffmayer, 2007). The extent to which these interactions among shark species determine nursery habitat use is largely unknown.

Because of this lack of information on habitat and resource partitioning among species using nursery habitats communally (DeAngelis et al., 2008), it has been suggested that there are advantages and disadvantages of communal use by more than one species. Adults of those species utilizing specific nursery habitats tend to avoid these habitats, resulting in reduced predation pressure (i.e., avoidance of cannibalism) for juveniles (Simpfendorfer and Milward, 1993; DeAngelis et al., 2008). Shallow water habitats in general are relatively inaccessible to

large adult sharks of any species, providing young sharks an area to escape inter- and intra-species predation. Disadvantages of several shark species within these nursery areas may be increased competition for resources, most notably food (Simpfendorfer and Milward, 1993; Bethea et al., 2004; DeAngelis et al., 2008). There is little information on the competition between shark species who exhibit diet overlap within these nursery areas. The occurrence of large congregations of multiple species may drive a level of prey selectivity by certain species in order to avoid competition and maximize prey availability.

Worldwide, shark nursery habitats have been impacted by human activities. The continuing industrialization and growth of human populations has increased habitat loss, eutrophication, sedimentation, overexploitation, and pathogenesis in coastal waters (Boynton et al., 1996; DeAngelis et al., 2008). The alteration, degradation, and loss of coastal habitats such as barrier islands are a major ecological concern because these areas provide protected, isolated habitats that cannot be found elsewhere along the coast (O'Connell et al., 2005; Heupel et al., 2007). For example, human use and development has transformed many barrier islands from dynamic natural ecosystems into intensively developed urban centers (Ray and Gregg, 1991). Commercial and industrial development along coastal waters makes essential fish habitats highly susceptible to a multitude of ecological problems (DeAngelis et al., 2008). Depressed oxygen conditions (hypoxia or anoxia) within estuarine and coastal ecosystems often results in the mortality of marine fauna (Boynton et al., 1991). Seagrass beds often serve as pupping and nursery habitats and the loss of these areas in bays and lagoons usually indicates increased eutrophication (Boynton et al., 1991; Gullström et al., 2002). Recent reports have uncovered widespread losses of seagrass habitats in coastal areas in North America, Australia, Europe, and Africa (Gullström et al., 2002). Finally, the destabilization of sediments within recently

disturbed habitats can affect not only seagrass beds, but can also alter or destroy other shark nursery habitats such as mangroves and coral reefs (Gullström et al., 2002).

The strong correlation between fish biomass and the productivity of seagrasses and mangroves emphasizes the important role these habitats have for coastal aquatic ecosystems (Gullström et al., 2002). This association is especially important for sharks that show a strong philopatric relationship to these regions that may have been historically a good nursery. Problems arise, though, when nurseries become altered and cannot provide the benefits they once offered (Heupel et al., 2007). The protection of limited nursery habitats such as coral reefs, seagrass beds, and mangroves within bays and lagoons is crucial to sustaining shark populations (DeAngelis et al., 2008). Many of the life history stages of sharks make them increasingly vulnerable to overexploitation by humans (Helfman et al., 1997). Fishing pressure has reduced shark populations drastically to the point where many species cannot withstand a fishing mortality of as low as 5% removal of the existing population each year (Helfman et al., 1997). Overfishing is threatening coastal and pelagic sharks to the point where several shark species are at risk of large scale extirpation (Baum et al., 2003). North American shark populations are rapidly declining (Helfman et al., 2005). Members of the genus *Carcharhinus* have declined substantially in the past decade with individual species declining anywhere from 49 to 83% (Baum et al., 2003). Coastal and pelagic shark populations in the Gulf of Mexico have declined 99% from historical population levels (Myers and Worm, 2005). The long-term loss and conversion of vegetated shallow-water habitats into deep-water, high wave energy and hard-bottom artificial substrates has resulted in the long-term decline of juvenile *C. leucas* in Lake Pontchartrain (O'Connell et al., 2007). Local management to protect shark populations and

habitats is insufficient due to long distance movements in international waters of many species (Helfman et al., 1997).

The lemon shark (*N. brevirostris*) is a large coastal species belonging to the family Carcharhinidae (Compagno, 1984). It can be found in three widely separated regions: the western Atlantic from New Jersey to Brazil, the west African coast, and the eastern Pacific from Baja California (including the Sea of Cortez) to coastal Columbia (Compagno, 1984). In particular, *N. brevirostris* is abundant in the shallow waters of the Caribbean and southern Florida (Cortés and Gruber, 1990). The species prefers clear coastal waters around reef systems and also occurs in seagrass habitats associated with mangroves (Knip et al., 2010). They have also been shown to tolerate brackish waters of estuaries and may enter freshwater at times (Knip et al., 2010). The importance of such habitats is indicated by the high-site fidelity for parturition exhibited by female *N. brevirostris* (Feldheim et al., 2001a; 2001b; 2002; Freitas et al., 2006). A typical example of these habitats occurs in the Bahamas at Bimini. This small chain of mangrove-fringed islands surrounds a shallow lagoon (Gruber et al., 2001; Feldheim et al., 2001b; 2002) and is utilized as a pupping ground and nursery for *N. brevirostris* (Gruber et al., 2001). Most of the available data on *N. brevirostris* behavior while in nursery habitats comes from this area.

Nurseries such as Bimini Lagoon are optimal habitats for newborn and sub-adult *N. brevirostris* for numerous reasons. The shallow water and mangrove fringed habitats provide protection from predation (Castro, 1993; Morrissey and Gruber, 1993b; DeAngelis et al., 2008). Depth has been shown to play a substantial role in predator avoidance and survival of young *N. brevirostris* in Bimini Lagoon (Morrissey and Gruber, 1993b). Young juvenile *N. brevirostris* remain in shallow water close to shore (Morrissey and Gruber, 1993a) to avoid the cannibalistic

tendencies of adult *N. brevirostris* and intraspecific predation of other large coastal sharks (Morrissey and Gruber, 1993b; Clermont and Gruber, 2005). Natural mortality for *N. brevirostris* within the first year of life ranges from 39 to 60% (Barker et al., 2005).

This species has a long history of cannibalistic tendencies where "shark-eat-shark" episodes have been observed in adult *N. brevirostris* during voracious feeding frenzies (Vorenberg, 1962). This cannibalistic tendency as well as intraspecific predation from larger predators on juvenile sharks is common in nursery areas (Morrissey and Gruber, 1993b). Neonatal and young of the year *N. brevirostris* are rarely observed outside the shallow seagrass flats and never in the deeper depth zones (DeAngelis et al., 2008) while larger, adult sharks are routinely observed on the reefs to at least 50-m as opposed to the shallow flats (Cortés and Gruber, 1990). The species appears to increase their habitat use into deeper waters as they get older and larger. This ontogenetic expansion has been exhibited by early juvenile *N. brevirostris* that were observed more frequently within deeper waters containing larger adult sharks (DeAngelis et al., 2008). Young *N. brevirostris* have also been observed routinely swimming or resting within the deep mangrove thicket (Morrissey and Gruber, 1993b) where larger sharks are unable to enter. Complex habitats such as mangroves have been well documented as a means of predator avoidance for many fish species (Morrissey and Gruber, 1993b).

Besides providing protection from predation, highly productive shallow water habitats also offer young sharks an abundance of food (Castro, 1993; Morrissey and Gruber, 1993b; DeAngelis et al., 2008). Mangroves and seagrass beds serve as nursery areas for many invertebrate and small fish species (Morrissey and Gruber, 1993b). These productive habitats are attractive to young *N. brevirostris* as nurseries because they require large amounts of food during their first few months of life to meet growth requirements (Castro, 1993; Morrissey and

Gruber, 1993b). Young *N. brevirostris* studied in the Florida Keys feed on small teleosts (both small schooling fishes and larger predatory fishes), amphipods, and various crustaceans (Cortés and Gruber, 1990). Typical schooling fishes are found in shallow seagrass beds and include killifish (Fundulus spp.), silversides (Menidia spp.), and mojarras (Gerreidae spp.; Cortés and Gruber, 1990; Motta et al., 1997). Predatory fishes are typically reported to nocturnally feed in seagrass beds and include seabreams (Sparidae spp.), snappers (Lutjanidae spp.), and grunts (Haemulidae spp.; Cortés and Gruber, 1990, Motta et al., 1997). Other prey items include schools of silver (*Mugil curema*) and striped mullet (*Mugil cephalus*), toadfish (*Opsanus beta*), pinfish (*Lagodon rhomboides;* Cortés and Gruber, 1990) crabs, and shrimp. Plant material accounts for 11% of the lemon shark diet as well (Wetherbee et al., 1990). Young *N. brevirostris* have shown no diel feeding periodicity also suggesting that feeding is asynchronous in the population (Cortés and Gruber, 1990). After feeding, *N. brevirostris* will completely or almost completely digest the prey before eating again (Cortés and Gruber, 1990; Wetherbee et al., 1990). As juveniles grow, this ontogenetic expansion to a variety of habitats allows the sharks to shift their diet (Cortés and Gruber, 1990). Compared to juveniles, the stomachs of large *N. brevirostris* (>140 cm PCL) have been found containing elasmobranchs, lobsters, and adult jacks, ordinarily found in deeper water (Cortés and Gruber, 1990). This ontogenetic change in both types and size of habitat provides an increase in prey availability and prey type (Cortés and Gruber, 1990). For example, *R. terraenovae* undergo an ontogenetic shift in their dietary habits, with young sharks feeding primarily on invertebrate prey and adult sharks feeding primarily on teleosts and elasmobranchs (Hoffmayer and Parsons, 2003).

Finally, female *N. brevirostris* nursery habitat selection critically influences adult fitness and recruitment rates through offspring growth and survival (Feldheim et al., 2001a; 2002).

Recent research has indicated substantial differences in growth rates of *N. brevirostris* at different nurseries (Feldheim et al., 2002; Barker et al., 2005). Differences in growth rates between juvenile *N. brevirostris* residing in nurseries in the Bahamas versus those found in the Florida Keys has been determined (Barker et al., 2005). Neonate *N. brevirostris* residing in the Florida Keys were significantly larger than those found in the Bahamas resulting in varying growth rates between nurseries in geographically distinct areas (Barker et al., 2005). There appears to be a strong directional selection against larger body size and fast growth rates in juvenile *N. brevirostris* within the nursery habitat of Bimini Lagoon (Dibattista et al., 2007). Small body size and slower growth rates early in life may be favorable phenotypes for *N. brevirostris* residing in Bimini. This could be due to specific selection pressures such as increased predation on individuals that take more risks during foraging or other environmental characteristics (Dibattisa et al., 2007). More information is needed on growth and diet of young *N. brevirostris* that occur in other known nursery habitats.

First reports of YOY and juvenile *N. brevirostris* at the Chandeleur Islands were made in 1972 from gill net and seine surveys within tidal creeks, channels, and open beaches during the summer months (Laska, 1973). Recent surveys conducted by the Nekton Research Laboratory (NRL) of the University of New Orleans have confirmed that the Chandeleur Islands, Louisiana contain nursery habitats for *N. brevirostris*. These islands are a 65 km long chain of barrier islands about 40 km off the Louisiana coast in the Gulf of Mexico (Michot and Nault, 1993). Unfortunately, these islands are one of the most rapidly receding barrier islands systems in the United States due to frequent hurricanes in the northern Gulf of Mexico and the lack of sand supply resulting in high erosion rates (Kahn, 1986). They are being transformed from a continuous barrier island arc into a series of small islands and shoals with a large number of tidal

channels and inlets. This is especially important because the landward migration of lagoons, bays, and barrier islands (Hayden et al., 1991) around the world could result in the loss of nursery habitat for many marine species, including sharks. The Chandeleur Sound contains deeper open water areas including tidal channels and bays as well as low relief flats and shallow bays. A change from protected, shallow habitats to a homogenous stretch of open, deep water would likely impact the reproduction of many fishes, including sharks, associated with the Chandeleur Islands. Chandeleur Sound is bordered by habitats that consist of several marsh plant species including black mangrove (*Avicennia germinans*) and salt marsh cordgrass (*Spartina alterniflora;* Kahn, 1986).

This area also contains five species of seagrasses, marsh flats, black mangroves, tidal channels, and surf zones. Mangroves and seagrass flats are important nursery grounds, feeding areas, and predation refuges for numerous fish and invertebrate populations (Boynton et al., 1996; Gullström et al., 2002). The diversity of habitats around the Chandeleur Islands provides coastal shark species a multitude of ecological choices, especially in regard to the diversity of prey items. Perhaps this partially explains why the shallow waters of the north Gulf of Mexico contain a species rich shark assemblage (Parsons and Hoffmayer, 2005). The Biloxi Marshes are another area in coastal Louisiana that provides coastal shark species an abundance of prey items and diverse habitats. The Biloxi Marshes span an area of 51,893 hectares of brackish (4-18 PSU) and intermediate (2-8 PSU) marshes in southern Louisiana (Maiaro, 2004). The wetlands are located on a complex of abandoned river deltas that is relatively undeveloped and degrading at a much slower rate than other wetlands in southern Louisiana (Maiaro, 2004). The Biloxi Marshes support extremely valuable fisheries including oysters, brown shrimp (*Farfante penaeus aztecus*), white shrimp (*Litopenaeus setiferus*), blue crab (*Callinectes sapidus*), spotted seatrout

(*Cynoscion nebulosus*), and red drum (*Sciaenops ocellatus*) as well as providing protection against hurricanes for St. Bernard and Orleans parishes (Maiaro, 2004). The brackish and saline ponds and bayous contain vast meadows of submersed aquatic vegetation (SAV), notably widgeon grass (*Ruppia maritima*) that serves as refugia for small fishes and crustaceans.

Further recent research by the NRL (C. Schieble, University of New Orleans, personal communication, 2008) has revealed that the Chandeleur Islands and Biloxi Marshes are home to various coastal shark species that play an integral role within these aquatic ecosystems. The following shark species are known to occur at the Chandeleur Islands: Atlantic sharpnose (*Rhizoprionodon terraenovae*), bonnethead (*Sphyrna tiburo*), spinner (*Carcharhinus brevipinna*), finetooth (*C. isodon*), bull (*C. leucas*), blacktip (*C. limbatus*), and *N. brevirostris*. The only shark species known to occur at both the Biloxi Marshes and Chandeleur Islands are *R. terraenovae, C. leucas,* and *C. limbatus*. Each of these species uses different habitats and prey items in this region of southeastern Louisiana and the four species most commonly collected by the NRL since 2003 were *N. brevirostris*, *R. terraenovae*, *C. leucas*, and *C. limbatus*.

The Atlantic sharpnose shark (*R. terraenovae*) is a small, abundant carcharhinid that inhabits coastal waters off the Atlantic and Gulf of Mexico (Bethea et al., 2006; Carlson et al., 2008). In the north central Gulf of Mexico juvenile and mature males recruit to coastal waters beginning in April, after which males migrate offshore to mate (Parsons and Hoffmayer, 2005). Males begin maturing at 60-65 cm TL and fully mature at approximately 80 cm TL (Parsons, 1983) or 2.0-2.4 years (Parsons, 1985). Females begin maturing at 60 cm TL and fully mature at approximately 85-90 cm TL (Parsons, 1983) or 2.4-2.8 years (Parsons, 1985). Mature females remain offshore never returning to inshore nursery habitats (Parsons and Hoffmayer, 2005). Neonates begin migrating in June from deeper waters into shallower, inshore nursery habitats

(Parsons, 1985; Parsons and Hoffmayer, 2005). All life stages are present in coastal waters by late June and generally remain inshore until they emigrate offshore in the fall (Bethea et al., 2006).

The bull shark (*C. leucas*) is one of the most common large sharks worldwide in tropical and subtropical coastal, estuarine, and some riverine environments (Simpfendorfer et al., 2005). One of the most common sharks in the near-shore coastal waters of the Northern Gulf of Mexico (Snelson et al., 1984), *C. leucas* can grow to a maximum size of 340 cm. Maturing and adult *C. leucas* primarily reside in deeper waters off the coast but do migrate into coastal and estuarine waters during the summer months (Snelson et al., 1984). Males reach maturity at approximately 160-225 cm TL and 180-230 cm TL in females (Simpfendorfer et al., 2005). Females carrying near-term embryos begin to appear in shallow, inshore waters in late April with parturition occurring in June and July (Snelson et al., 1984). All life stages are present in coastal waters by late June and generally remain inshore until they emigrate offshore to warmer southern waters.

The blacktip shark (*C. limbatus*) is a common shark species distributed in all tropical and subtropical continental waters (Killam and Parsons, 1989). In particular, *C. limbatus* are very common inhabitants of inshore coastal and estuarine regions in the Northern Gulf of Mexico (Killam and Parsons, 1989; Barry et al., 2008). Maturing and adult *C. limbatus* begin a northward migration from their wintering grounds in early March to mating and birthing areas (Castro, 1996). Males mature at approximately 143-145 cm TL (Castro, 1996) or 4-5 years of age and 156 cm TL (Castro, 1996) or 6-7 years in females (Killam and Parsons, 1989). Parturition occurs in shallow coastal waters from early May to early June with young remaining in the nursery habitats until fall (Killam and Parsons, 1989).

The objectives of my research were to examine the diet and prey availability for young of the year and juvenile *N. brevirostris* within the newly discovered nursery area of the Chandeleur Sound. The identification of these islands as a nursery area for *N. brevirostris* has many important implications. It offers the opportunity to compare the diet of the extensively studied nurseries in Bimini (Bahamas) and the Florida Keys with the nursery at the Chandeleur Islands. Because of the presence of other shark species, I was also interested in whether possible inter-species interactions or prey availability determine where *N. brevirostris* and three other locally common species (*R. terraenovae*, *C. leucas,* and *C. limbatus*) occur within the eastern portion of Pontchartrain Basin. If predation pressure from larger sharks is confining *N. brevirostris* to the Chandeleur Islands, then local conservation of this species will be directly influenced by populations of these other sharks. If, however, diet appears more important in determining the distribution of *N. brevirostris,* then conserving the local prey items would be more important for protecting this species. Finally, I was also interested in determining if the diets of any of these four species overlapped suggesting possible competition pressure. If these competitive interactions exist, then the continued use of the Chandeleur Islands as a *N. brevirostris* nursery could be determined by these other species. More specifically, my goals were to:

1. Measure diet and prey availability for young of the year and juvenile *N. brevirostris* at the Chandeleur Islands;
2. Use distribution data to determine whether prey availability influences occurrence for all four shark species; and
3. Test for diet resource partitioning between *N. brevirostris* and *R. terraenovae*

Materials and Methods

Diet and Prey Availability of Young N. brevirostris *at the Chandeleur Islands*

Source and handling of sharks – Field sampling at the Chandeleur Islands began in May 2009 and ended in August 2010. Sampling trips typically lasted four days and occurred during the following periods: 9-12 May 2009, 8-11 June 2009, 12-15 July 2009, 20-23 August 2009, 17-20 May 2010, 12 June 2010 (single day trip with an ABC News film crew), and 19-22 August 2010. Collection efforts typically began at 0800 and concluded at approximately 1700 each day. Young of year (YOY) and juvenile *N. brevirostris* were caught using rod and reel throughout the habitats at the Chandeleur Islands. Sight fishing for young *N. brevirostris* was done on a 2.44 m step ladder strapped onto a 4.88 m Carolina skiff boat (Figure 1). As one person poled the boat through the shallow water habitats, the second person looked for young *N. brevirostris* from atop the ladder. Each person was equipped with a 2.13 m spinning rod with 13.6 kg braided fishing line attached to a steel leader with a 3/0 J-hook. Hooks were baited with dead pinfish (*Lagodon rhomboides*) that were pitched out in front of the shark for attraction. After the shark was allowed to bite and chew on the bait for approximately 30 s, the hook was set and sharks were brought back to the boat for processing. Sharks were removed from hooks and weighed, measured, sexed, identified as to time and place of capture, and marked with a Wildlife Computers 12 mm passive integrated transponder tag (Figure 2).

To obtain diet samples, each shark was positioned vertically snout down over a 50 mm sieve screen. When the shark was immobilized, a small diameter nozzle head from a Chapin SureSpray model #20010 3.8 L pesticide sprayer was carefully inserted through the mouth down

Figure 1: Sight fishing atop a 2.44 m ladder in a 4.88 m Carolina skiff for young *N. brevirostris* at the Chandeleur Island nursery habitat.

Figure 2: Juvenile *N. brevirostris* with tools for data collection on the deck of the Carolina skiff. Sharks were also weighed (g), fin clipped, marked with a passive integrated transponder tag, stomach lavaged for gut contents, and then released.

to the stomach. A thin line of water flushed all stomach contents down towards the esophagus after which a pair of forceps was inserted into the mouth, opening the throat closure washing all contents onto a 50 mm sieve screen. The recovered contents were stored in plastic containers with 250 ml of ethanol. All sharks were released after they had fully recovered and were able to swim away on their own. A stomach lavage technique was utilized after talking with Dr. Eric Hoffmayer who had success with the method of collecting stomach contents in *C. leucas* (Eric Hoffmayer, University of Southern Mississippi personal communication 2009). The stomach eversion technique was not utilized because it is one that requires experience and careful handling while performing (Eric Hoffmayer, University of Southern Mississippi personal communication 2009). This new stomach lavage technique ensures the rapid collection of all stomach contents and does not require the use of MS-222 which can harm sharks rather than help (ASIH, 2003). This approach also promoted the rapid recovery and release of all sharks (Figure 3). The American Society of Ichthyologists and Herpetologists mandates that researchers need to take great care to avoid inducing stress in experimental subjects (especially on a prolonged basis) because it can evoke physiological and behavioral changes (ASIH, 2003). Furthermore, ASIH (2003) states that the benefits of anesthesia and potential effects on data should be weighed against the potential effects on the subject fish such that it avoids prolonged stressful restraint (ASIH, 2003).

Figure 3: Image of young *N. brevirostris* after being released unharmed and fully recovered at the Chandeleur Islands.

To determine prey availability, potential prey items were collected from the point of shark capture using a 15 m beach seine. At each capture site, three replicate seine hauls were made immediately following processing of the shark. All fishes collected were anesthetized with sodium bicarbonate and placed on ice. Afterward, these fishes were identified, counted, weighed, and measured.

Laboratory and data analysis – Identification of stomach contents was carried to the lowest possible taxonomic level. For each item, excess water was removed by blotting it on filter paper. The wet weight was determined by weighing on an OHAUS Scout Pro model SP402 400 g electronic balance to the nearest 0.1 g. In addition, the total length (TL) of each food item was taken when possible. The contribution of different prey items to the shark's diet was determined using standard quantitative methods (Cortes and Gruber, 1990; Newman et al., 2010). For each shark's diet, I calculated: 1 numerical importance (%N), the number of prey items in each category, expressed as a percentage of the total number of prey items; 2 frequency of occurrence (%F), the ratio of stomachs containing a specific prey compared to the total number of shark stomachs containing prey and expressed as a percentage (the sum of the values will exceed 100% because several prey types can be found simultaneously in a single stomach); 3 gravimetric importance (%W), the wet weight of a prey category compared to the total weight of the stomach contents, expressed as a percentage; and 4 index of relative important (%IRI), which is calculated as

$$IRI = \%O \times (\%N + \%W)$$

and

$$\%IRI_i = 100\ IRIi / \sum_1^n IRIi,$$

where n is the number of different food types.

Distribution and Prey Selectivity of Four Shark Species

Sampling – Fish assemblages were collected from 2004-2010 at designated sites between March and November from the Chandeleur Islands and Biloxi Marshes of Lake Borgne (Figure 4). Chandeleur Island sites were located at:

C-1 – 30°0.068'N 88°51.102'W

C-2 – 29°57.277'N 88°49.924'W

C-3 – 29°52.663'N 88°49.745'W

C-4 – 29°53.190'N 88°49.832'W (*Replaced site C-1 after Hurricane Katrina in August 2005*)

Biloxi Marsh sites were located at:

B-1/Half Moon Island – 30°7.875'N 89°26.717'W

B-2/Grand Pass – 30°7.570'N 89°13.878'W

P-9/Rigolets – 30°7.846'N, 89°38.855'W.

Fishes were caught using trawl, gillnet, and beach seining gear from three designated sites at each locality. Trawling was performed with a 4.9 m otter trawl with a 25.4 mm stretched mesh and a 1.8 m long cod end with 9.5 mm mesh by towing at 1.8 m/s for 10 min covering a distance of about 1.2 km. Gillnetting was performed with a gill net 100 m in length and 2 m in height, containing six alternating panels of 5.1 and 24.4 cm mesh, set for one hour. Seining was performed with a 15.2 m X 1.83 m bag seine with 9.5 mm mesh for 50 m perpendicular and onto the shore. Three replicate samples of each gear type were taken at each site after which all fishes were anesthetized with sodium bicarbonate and fixed in formalin. All fishes were brought back

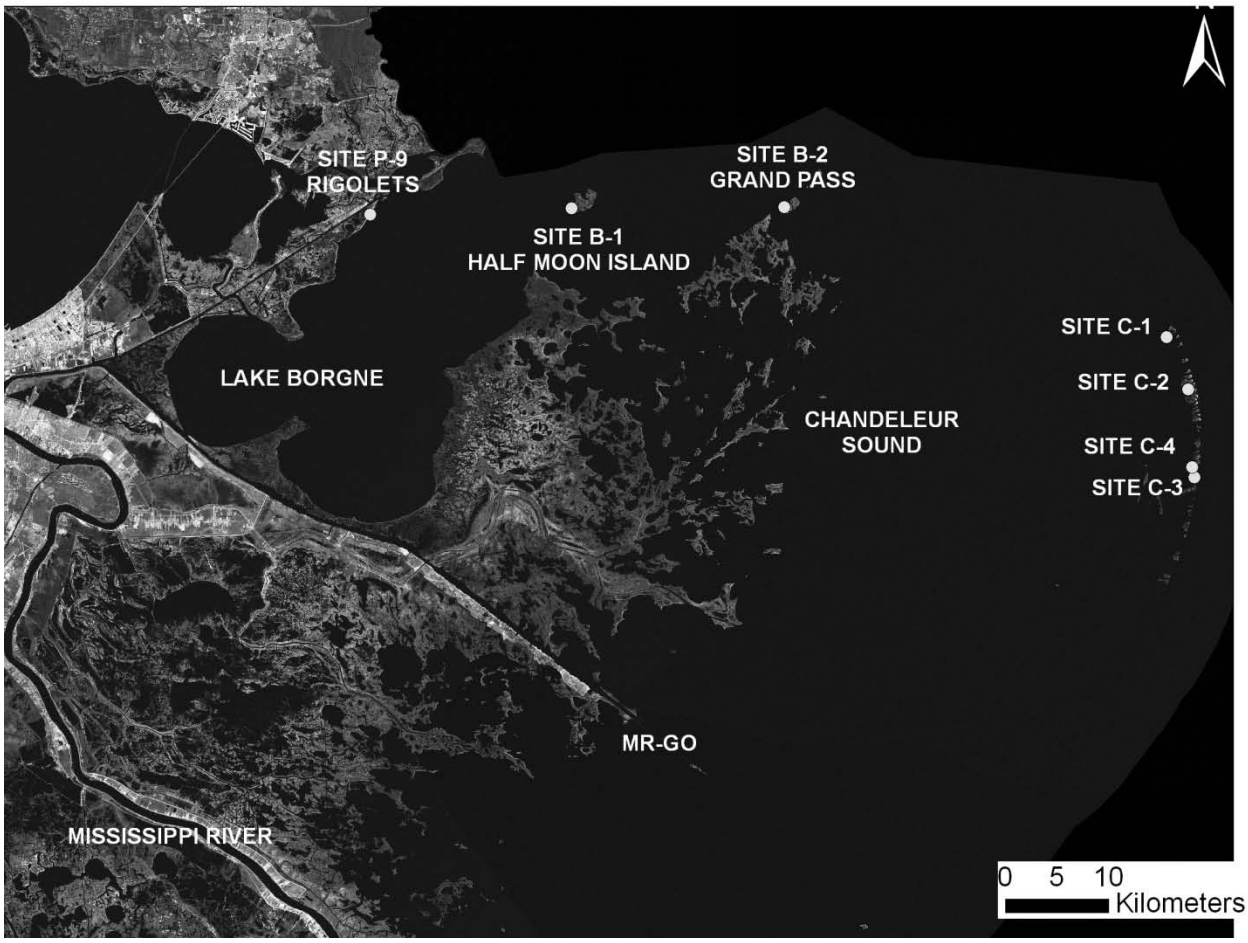

Figure 4: Map of the Chandeleur Islands and Biloxi Marshes in southeastern coastal Louisiana. Sampling stations used in the current survey are shown.

to the laboratory, rinsed in tap water, identified to the lowest possible taxonomic level, counted, measured, and weighed.

For all four shark species of interest (*N. brevirostris, R. terraenovae, C. limbatus,* and *C. leucas*), I mapped their occurrences at theses seven sites. The purpose of this mapping was to determine which species were widespread (i.e., occurred at all or most sites) and which were confined to specific coastal areas. Because temperature and salinity may determine which habitats sharks occupy (Parsons and Hoffmayer, 2005; Heupel and Simpfendorfer, 2008), I also compared ranges of temperature and salinity where each of these species occurred in southeastern Louisiana. If either of these variables were determining shark distributions then these data would elucidate these relationships.

Data Analysis – Fish assemblage samples from March to November from 2004 to 2010 from the Chandeleur Islands and Biloxi Marshes were compared using assemblage analysis procedures in the PRIMER (Plymouth Routines in Multivariate Ecological Research) 5.2.2 statistical package. Fish assemblage samples containing *N. brevirostris, R. terraenovae, C. limbatus,* or *C. leucas* during the various periods in the current study were compared using a non-metric multidimensional scaling (MDS) plot, analysis of similarity (ANOSIM, $\alpha = 0.05$), and analysis of dissimilarity (SIMPER). These four shark species are the most abundant species of shark, showing an overlap of habitat utilization and prey selectivity at the Chandeleur Islands and Biloxi Marshes. The purpose of these analyses was to determine if any of the shark species appeared to 'track' or 'follow' their preferred prey species. More simply, I asked whether these shark species occurred more with their preferred prey species versus other available species. First, a non-metric multidimensional scaling (MDS) plot was constructed to visually explore relationships among samples and determine if further comparative analyses were necessary. For

ANOSIM, similarity matrices were generated for fish assemblages by square root transforming the raw abundance data and calculating Bray-Curtis similarity indices for each pair-wise assemblage comparison. For SIMPER, dissimilarity matrices were generated for fish assemblages by square root transforming the raw abundance data to determine which fish species were most associated with differences in shark occurrences. I also performed a BIOENV routine to determine whether temperature, salinity, dissolved oxygen, turbidity, or the percentage of the preferred prey items of the four shark species influenced any of the observed significant differences among fish assemblages. Percentages of preferred prey items of each shark species were determined by selecting the top five fishes through literature review or available gut content in the diet of each shark species (Darnell, 1958; Snelson et al., 1984; Hoffmayer and Parsons, 2003; Bethea et al., 2004; Bethea et al., 2006; Barry et al., 2008). The frequency of occurrence of those species was calculated for each sample of fish assemblages. The idea here was to use the combined percentage of the preferred prey items index as a potential environmental indicator to test for possible 'tracking' of preferred prey by a shark species. The BIOENV test determines the relationship among assemblage data and environmental variables measured, including the preferred prey items index.

Assessing Resource Partitioning between N. brevirostris *and* R. terraenovae

The University of Southern Mississippi's Gulf Coast Research Laboratory (GCRL) in Ocean Springs, Mississippi longlined for sharks in Chandeleur Sound in the summers of 2009 and 2010. Twenty-five *R. terraenovae* were sacrificed for stomach contents to determine diet. Identification of stomach contents was carried to the lowest possible taxonomic level at GCRL and the data was provided to me by Dr. Eric Hoffmayer. Stomach contents of *R. terraenovae*

were analyzed identically to those of *N. brevirostris* in order to assess resource partitioning between the two shark species. Cumulative prey curves from stomach contents of *R. terraenovae* and *N. brevirostris* were constructed to determine if an adequate number of stomachs had been collected to accurately describe diets.

Results

Diet of Young N. brevirostris *at the Chandeleur Islands*

A total of 81 young lemon sharks (41 male and 40 female) were caught at the Chandeleur Island sampling sites in 2009 and 2010 (Figure 5). Forty of these were collected during four trips in 2009 and the remaining 41 sharks were collected during two trips in 2010. The Deepwater Horizon oil spill occurred on 20 April 2010 after the rig exploded resulting in 780 X 10^3 m^3 of crude oil leaking out into the Gulf of Mexico (RestoreTheGulf.gov, 2010). The spill prevented sampling trips in June and July to the Chandeleur Islands due to an inability to access our normal accommodations.

Young *N. brevirostris* ranged in size from 480-1220 mm FL and 30 out of 81 sharks contained stomach contents (Table 1). Teleost fishes were the primary prey item for these 30 YOY and juvenile *N. brevirostris* (Table 2) and these represented the largest portion of prey items by number (81%), frequency of occurrence (90%), weight (93.5%), and index of relative importance (98.2%; Table 3). The remaining stomach contents consisted of crustaceans and angiosperm plant material. A total of five fish species, two crustaceans, and three seagrasses were identifiable in the stomach contents of young *N. brevirostris*. The identifiable fishes were pinfish (*Lagodon rhomboides;* 12.1% I_{RI}), longnose killifish (*Fundulus similis*; 4.1% I_{RI}), inland

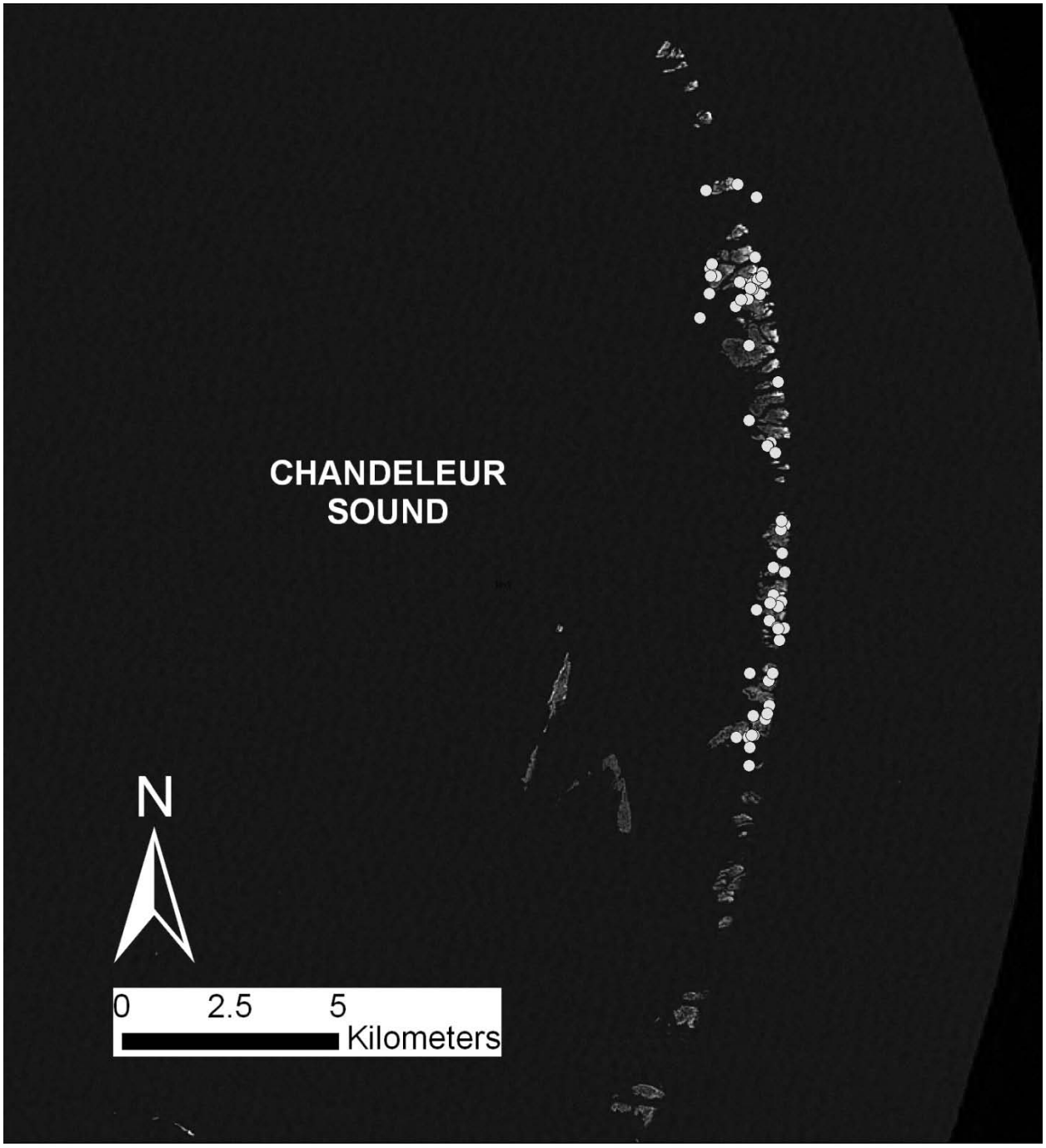

Figure 5: Map of the Chandeleur Islands, Louisiana. Points indicate collection localities of *N. brevirostris* during the summers of 2009 and 2010.

Table 1: Biological data on 81 young *N. brevirostris* (41 male and 40 female) collected at the Chandeleur Islands, Louisiana between 2009 and 2010. Thirty of these sharks contained stomach contents. ND = No Data.

Identific. Number	Date	Total Weight (g)	FL (cm)	Sex	Stomach Contents?
MC1	10-May-09	1420	550	Female	No
MC2	11-May-09	1500	560	Female	Yes
MC3	11-May-09	1670	580	Female	Yes
MC4	11-May-09	3000	680	Female	Yes
MC5	11-May-09	1800	536	Female	Yes
MC6	11-May-09	1580	560	Female	No
MC7	11-May-09	ND	550	Male	Yes
JC1	8-Jun-09	1720	565	Male	No
JC2	9-Jun-09	2090	605	Female	No
JC3	9-Jun-09	8640	990	Female	No
JC4	9-Jun-09	2110	585	Male	No
JC5	9-Jun-09	1510	560	Female	Yes
JC6	9-Jun-09	2170	600	Male	Yes
JC7	9-Jun-09	2550	688	Male	No
JC8	10-Jun-09	1550	540	Female	No
JC9	10-Jun-09	2050	586	Male	Yes
JC10	10-Jun-09	3900	710	Female	No
JC11	10-Jun-09	6000	872	Male	Yes
JC12	8-Jun-09	1750	626	Male	Yes
JC13	11-Jun-09	ND	1220	Male	Yes
JuC1	13-Jul-09	1650	570	Female	No
JuC2	13-Jul-09	1300	505	Female	No
JuC3	14-Jul-09	1875	575	Female	Yes
JuC4	14-Jul-09	1525	529	Male	Yes
JuC5	12-Jul-09	1900	530	Male	No
JuC6	15-Jul-09	1700	535	Female	No
JuC7	15-Jul-09	1600	542	Male	No
AC1	20-Aug-09	3175	690	Male	Yes
AC2	20-Aug-09	4700	805	Male	No
AC3	20-Aug-09	~6000	865	Female	No
AC4	21-Aug-09	~6000	1065	Male	No
AC5	21-Aug-09	2910	662	Male	Yes

Table 1: Continued

AC6	21-Aug-09	1900	573	Male	Yes
AC7	22-Aug-09	2320	590	Female	No
AC8	22-Aug-09	~8000	1035	Male	No
AC9	22-Aug-09	1750	536	Male	Yes
AC10	22-Aug-09	2310	616	Male	No
AC11	20-Aug-09	3750	710	Male	Yes
AC12	21-Aug-09	1700	570	Female	No
AC13	22-Aug-09	1700	553	Female	Yes
AC14	22-Aug-09	3550	682	Male	No
M2C1	17-May-10	3400	735	Female	No
M2C2	17-May-10	6020	885	Male	No
M2C3	18-May-10	2350	640	Female	Yes
M2C4	18-May-10	2450	620	Male	No
M2C5	18-May-10	2250	605	Female	Yes
M2C6	18-May-10	1600	590	Female	No
M2C7	18-May-10	6540	815	Male	No
M2C8	19-May-10	1520	548	Female	No
M2C9	19-May-10	6500	935	Male	No
M2C10	19-May-10	2450	622	Male	No
M2C11	19-May-10	2070	685	Female	Yes
M2C12	19-May-10	4500	757	Female	No
M2C13	19-May-10	1600	568	Male	No
M2C14	17-May-10	1600	570	Male	No
M2C15	17-May-10	1800	585	Female	No
M2C16	18-May-10	1700	610	Male	No
M2C17	18-May-10	1950	600	Male	No
M2C18	18-May-10	900	580	Female	No
M2C19	18-May-10	5200	860	Female	No
M2C20	18-May-10	1600	610	Male	No
M2C21	18-May-10	6600	850	Female	No
M2C22	18-May-10	800	530	Female	No
M2C23	18-May-10	6000	900	Male	No
M2C24	19-May-10	1100	550	Female	No
M2C25	20-May-10	1200	620	Female	Yes
J2C1	12-Jun-10	1350	480	Male	No
A2C1	20-Aug-10	2500	648	Male	No
A2C2	20-Aug-10	1250	570	Male	Yes
A2C3	20-Aug-10	1490	510	Male	Yes

Table 1: Continued

A2C4	20-Aug-10	2350	593	Male	Yes
A2C5	20-Aug-10	2925	640	Male	Yes
A2C6	20-Aug-10	1500	515	Female	No
A2C7	20-Aug-10	2015	587	Male	No
A2C8	20-Aug-10	2505	615	Female	Yes
A2C9	21-Aug-10	6000	860	Female	No
A2C10	21-Aug-10	6000	855	Female	No
A2C11	21-Aug-10	1550	510	Female	Yes
A2C12	21-Aug-10	2100	570	Female	No
A2C13	20-Aug-10	1500	570	Female	Yes
A2C14	20-Aug-10	1000	540	Female	No
A2C15	21-Aug-10	>6000	1110	Female	No

Table 2: Stomach contents of 30 *N. brevirostris* (16 male and 14 female) collected at the Chandeleur Islands between 2009 and 2010.

Identification Number	Contents	Weight (g)
MC2 (female)	*Fundulus similis*	9.47
	Lagodon rhomboides	1.64
	Lagodon rhomboides	2.17
MC3 (female)	*Callinectes sapidus*	2.30
MC4 (female)	Unknown fish muscle	0.41
MC5 (female)	*Strongylura marina*	27.92
MC7 (male)	*Menidia beryllina*	1.94
	Menidia beryllina	2.70
	Menidia beryllina	2.08
	Menidia beryllina	1.79
	Menidia beryllina	3.70
	Menidia beryllina	1.26
	Menidia beryllina	1.80
	Menidia beryllina	2.48
	Menidia beryllina	2.06
	Synodus foetens	0.97
	Fundulus similis	3.17
	Lagodon rhomboides	2.03
JC5 (female)	*Fundulus similis*	3.32
JC6 (male)	Unknown fish muscle	0.44
JC9 (male)	*Callinectes sapidus*	3.24
JC11 (male)	Unknown fish bones	1.45
JC12 (male)	Unknown fish muscle	0.97
JC13 (male)	*Lagodon rhomboides*	2.43
JuC3 (female)	Unknown fish muscle	2.83
	Unknown fish muscle	0.98
	Unknown fish muscle	0.75
	Unknown fish muscle	0.85
JuC4 (male)	Unknown fish muscle	0.24
AC1 (male)	Unknown fish muscle	0.31
AC5 (male)	*Halodule wrightii*	0.10
	Thalassia testudinum	0.27
	Syringodium filiforme	0.08
	Unknown fish gills	1.06
AC6 (male)	*Syringodium filiforme*	0.36
	Thalassia testudinum	0.10
AC9 (male)	Unknown fish muscle (pelvic girdle)	3.63
AC11 (male)	Unknown fish muscle	0.18

Table 2: Continued

AC13 (female)	Unknown fish muscle	0.38
	Penaeidae sp.	0.08
M2C3 (female)	Unknown fish fins	2.34
M2C5 (female)	*Lagodon rhomboides*	1.2
M2C11 (female)	*Callinectes sapidus*	0.38
M2C25 (female)	*Lagodon rhomboides*	2.40
A2C2 (male)	Unknown fish bones	2.46
A2C3 (male)	Unknown fish muscle	0.33
A2C4 (male)	Unknown fish muscle	0.18
A2C5 (male)	*Lagodon rhomboides*	0.86
A2C8 (female)	*Lagodon rhomboides*	1.49
	Unknown fish muscle	0.65
A2C11 (female)	*Menidia beryllina*	0.70
	Unknown fish muscle	3.12
	Thalassia testudinum	0.27
A2C13 (female)	Unknown fish muscle	0.71

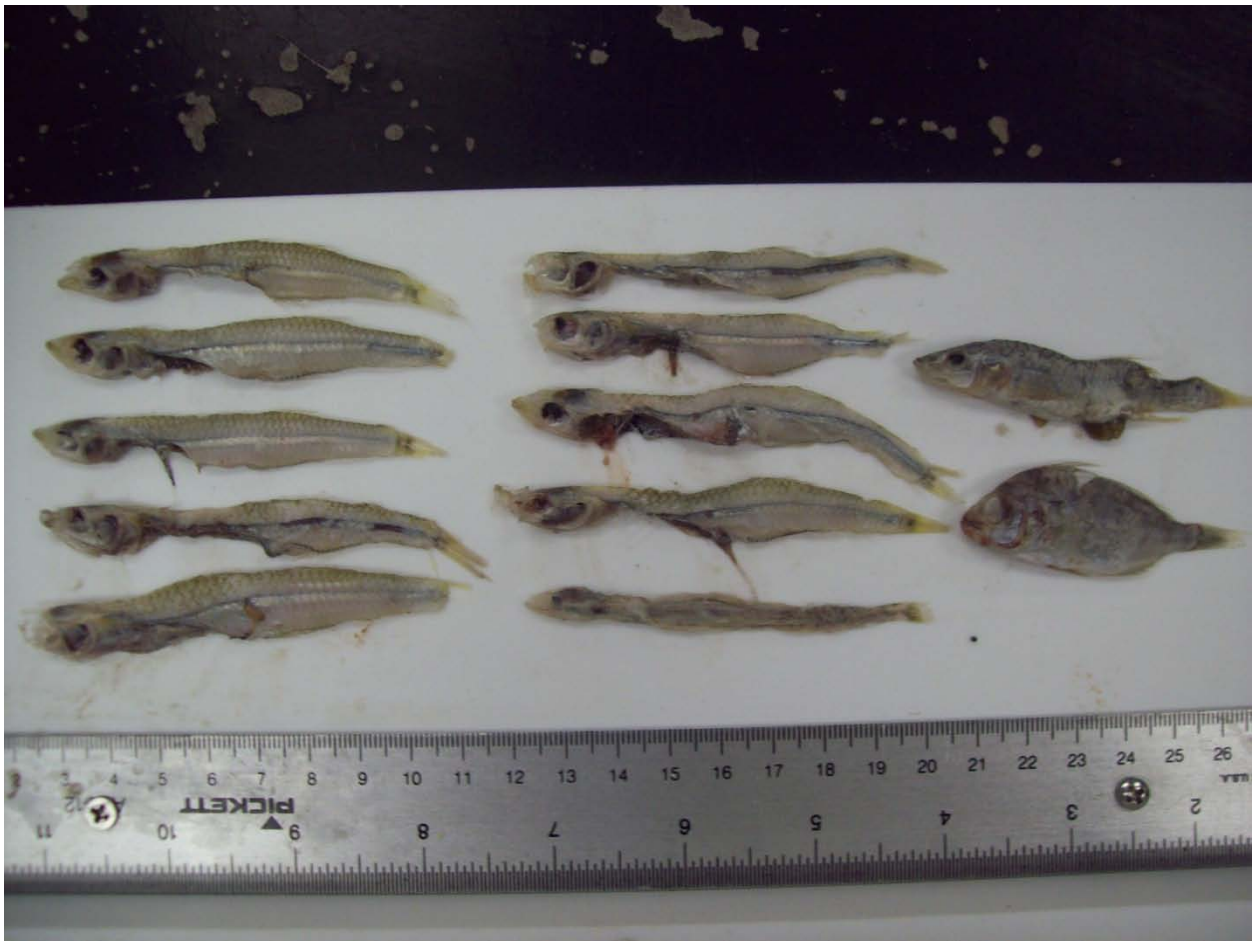

Figure 6: Stomach contents from young *N. brevirostris* at the Chandeleur Island nursery habitat in May 2009. Diet composed of *L. rhomboides, M. beryllina, F. similis,* and *S. foetens*.

Table 3: Diet composition of YOY and young *Negaprion brevirostris* collected at the Chandeleur Islands, Louisiana from 2009 to 2010 (n=30)

Food item	N	%	F	%	wt (g)	%	IRI	%IRI
Teleost	43	81.1%	27	90.0%	104.0	93.5%	1.6	98.2
Fundulus similis	3	5.7%	3	10.0%	16.0	14.4%	0.0	4.1
Lagodon rhomboides	7	13.2%	7	23.3%	13.4	12.0%	0.1	12.1
Menidia beryllina	10	18.9%	2	6.7%	20.5	18.4%	0.0	5.1
Strongylura marina	1	1.9%	1	3.3%	27.9	25.1%	0.0	1.9
Synodus foetens	1	1.9%	1	3.3%	1.0	0.9%	0.0	0.2
Unid teleosts	21	39.6%	17	56.7%	25.3	22.8%	0.4	72.6
Crustacean	4	7.5%	4	13.3%	6.0	5.4%	0.0	1.1
Callinectes sapidus	3	5.7%	3	10.0%	5.9	5.3%	0.0	2.3
Penaeidae sp.	1	1.9%	1	3.3%	0.1	0.1%	0.0	0.1
Angiospermi	6	11.3%	3	10.0%	1.2	1.1%	0.0	0.8
Halodule wrightii	2	3.8%	1	3.3%	0.1	0.1%	0.0	0.3
Syringodium filiforme	2	3.8%	2	6.7%	0.4	0.4%	0.0	0.6
Thalassia testudinum	2	3.8%	3	10.0%	0.6	0.6%	0.0	0.9

silverside (*Menidia beryllina*; 5.1% I_{RI}), Atlantic needlefish (*Strongylura marina*; 1.9% I_{RI}), and inshore lizardfish (*Synodus foetens*; 0.2% I_{RI}; Figure 6). The identifiable crustaceans were blue crab (*Callinectes sapidus*; 2.3% I_{RI}) and penaeid shrimp (*Penaeidae sp.*; 0.1% I_{RI}). The identifiable seagrasses were manatee grass (*Syringodium filiforme*; 0.6% I_{RI}), turtle grass (*Thalassia testudinum*; 0.9% I_{RI}), and shoal grass (*Halodule wrightii*; 0.3% I_{RI}).

Prey availability was determined by seining in areas throughout the Chandeleur Islands where young *N. brevirostris* were collected (n=15). The most abundant prey item collected by number was brown shrimp (*Farfante penaeus aztecus),* followed by pinfish (*L. rhomboides*), scaled sardine (*Harengula jaguana*), southern kingfish (*Menticirrhus americanus*), and white mullet (*Mugil curema*; Table 4). The most abundant prey items collected by frequency of occurrence were *C. sapidus* and *M. curema* followed by longnose killifish (*Fundulus similis*), inland silverside (*Menidia beryllina*), and Florida pompano (*Trachinotus carolinus*; Table 4). The diet of young *N. brevirostris* at the Chandeleur Islands was composed of the more abundant prey items within the nursery habitat. Investigating this further, by combining the trawl, gillnet, and seine samples from the Chandeleur Islands from March – November of 2004-2010, the three most abundant prey items found in the diet of young *N. brevirostris* rank in the top ten of most abundant fishes collected (Table 5). The most abundant prey item in the diet of young *N. brevirostris* at the Chandeleur Islands is *L. rhomboides* which is ranked number one (49.57%), along with *M. beryllina* ranked number three (5.71%), and *F. similis* number ten (1.72%; Table 5).

Distribution and Prey Selectivity of Four Shark Species

A total of 92,836 fishes comprising 117 species were collected at sites in the Chandeleur Islands

Table 4: Prey availability determined by seining (n=15) habitats young lemon sharks were captured in. Abundance of prey items is presented in percent by number (%N) and percent frequency of occurrence (%F). Asterisks indicate prey items found in the diet of young lemon sharks at the Chandeleur Island nursery habitat.

Species	**%N**	**%F**
Anchoa hepsetus	0.02%	6.70%
Bairdiella chrysoura	0.45%	6.70%
*Callinectes sapidus**	0.26%	53.30%
Caranx hippos	0.16%	26.70%
Cyprinodon variegatus	0.06%	6.70%
Evorthodus lyricus	0.24%	6.70%
*Farfante penaeus aztecus**	41.35%	20.00%
*Fundulus similis**	1.46%	46.70%
Gobionellus boleosoma	0.06%	13.30%
Harengula jaguana	11.58%	13.30%
Hyphorhampus unifasciatus	0.04%	6.70%
*Lagodon rhomboides**	17.70%	26.70%
Larimus fasciatus	0.18%	13.30%
Leiostomus xanthurus	1.12%	26.70%
*Menidia beryllina**	5.35%	46.70%
Menticirrhus americanus	11.36%	20.00%
Mugil cephalus	0.10%	6.70%
Mugil curema	7.56%	53.30%
Sciaenops ocellatus	0.02%	6.70%
*Synodus foetens**	0.08%	13.30%
Trachinotus carolinus	0.83%	33.30%

Table 5: The ten most abundant fish species collected at the Chandeleur Islands, Louisiana in the months of March through November from 2004 to 2010 represented in percent by number (%N). Prey items found in the diet of YOY and young lemon sharks at the Chandeleur Islands are indicated (*).

Species	**%N**
*Lagodon rhomboides**	49.57%
Eucinostomus gula	12.84%
*Menidia beryllina**	5.71%
Leiostomus xanthurus	4.40%
Bairdiella chrysoura	3.93%
Mugil curema	3.63%
Anchoa hepsetus	3.06%
Anchoa mitchilli	2.06%
Harengula jaguana	1.85%
*Fundulus similis**	1.72%

and Biloxi Marshes from 2004 to 2010. The most abundant shark species caught was *R. terraenovae* (30), followed by *C. leucas* (20), *C. limbatus* (19), and *N. brevirostris* (17). Site C-3 at the Chandeleur Islands had the highest abundance of *R. terraenovae*, which was also collected at sites C-1, C-2, C-4, and B-2. The most widely occurring species was *C. leucas* which was collected at all seven sampling sites and appeared evenly distributed both at the Chandeleur Islands and Biloxi Marshes. *Carcharhinus limbatus*, which was also widespread, was collected at sites C-3, C-4, and B-1. The distribution of *C. limbatus* was similar to that of *R. terraenovae* with occurrences at all four Chandeleur Island sites as well as at site B-2 at Grand Pass and B-1 at Half Moon Island with sites B-2 and C-1 having the highest abundance of this species. Site C-2 at the Chandeleur Islands had the highest abundance of *N. brevirostris*. This species was also collected at sites C-1, C-3, and C-4. This was the only species not collected in any of the Biloxi Marsh sites.

There was substantial overlap in temperature ranges for all four shark species, although *N. brevirostris* appeared to prefer higher temperatures than the other species and was not collected at temperatures less than 27 °C (Table 6). The other three species were not collected in temperatures lower than 19.1 to 21.2 °C (Table 6). No sharks were caught in water greater than 32° C. Salinity ranges showed more notable differences among shark species with *N. brevirostris* and *R. terraenovae* restricted to smaller ranges of higher salinities while *C. leucas* and *C. limbatus* occurred in most available salinities, including oligohaline conditions (Table 6).

An MDS plot of fish assemblage centroids revealed potential differences in prey availability among sites associated with different shark species (Figure 7). Pair-wise comparisons of fish assemblages (i.e., potential prey species) associated with each shark species

Table 6: Temperature and salinity ranges for shark occurrences at the Chandeleur Islands and Biloxi Marshes.

Species	Temperature Range (°C)	Salinity Range (PSU)
Negaprion brevirostris	27.2 – 32.0	19.0 – 32.0
Rhizoprionodon terraenovae	19.8 – 32.0	20.4 – 32.1
Carcharhinus leucas	19.1 – 32.0	2.2 – 27.5
Carcharhinus limbatus	21.2 – 32.0	4.3 – 31.6

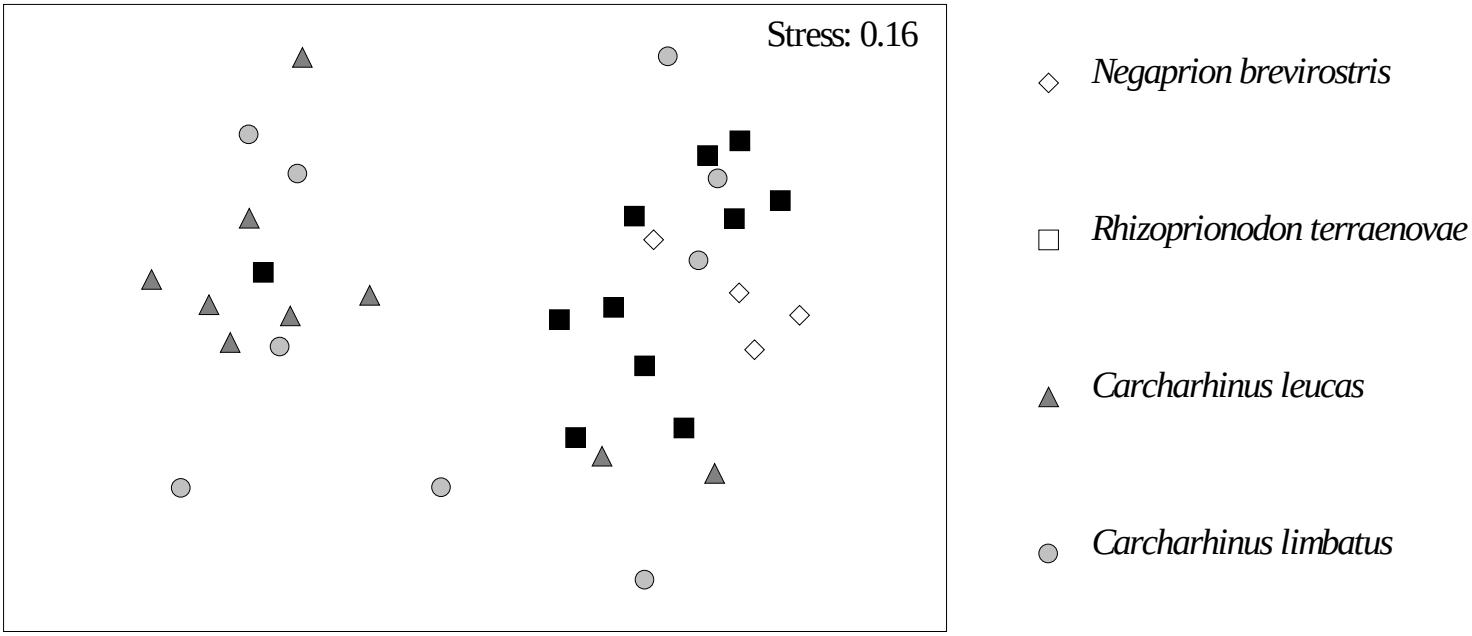

Figure 7: Non-metric multidimensional scaling (MDS) plot of fish assemblages associated with four shark species (*Negaprion brevirostris, Rhizoprionodon terraenovae*, *Carcharhinus leucas*, and *C. limbatus*) collected at the Chandeleur Islands and Biloxi Marshes between 2003 and 2010. Distances between symbols represent similarities (i.e., closer symbols represent similar assemblage compositions).

yielded four significant ($p < 0.05$) differences (Table 7). Fish assemblages associated with *N. brevirostris* were significantly different (ANOSIM, $R=0.562$, $p < 0.01$) than fish assemblages associated with *C. leucas* (Table 7). Fish assemblages associated with *R. terraenovae* were significantly different (ANOSIM, $R=0.516$, $p < 0.01$) than fish assemblages associated with *C. leucas* (Table 7). Fish assemblages associated with *R. terraenovae* were also significantly different (ANOSIM, $R=0.271$, $p < 0.01$) than fish assemblages associated with *C. limbatus* (Table 7). A fourth significant difference (ANOSIM, $R=0.514$, $p < 0.01$) occurred between collections where both *R. terraenovae* and *C. limbatus* were collected together and assemblages associated with *C. leucas* (Table 7).

SIMPER analysis of dissimilarity between occurrences of *C. leucas* versus *N. brevirostris* revealed marked differences in numbers of three primary prey items of YOY *N. brevirostris* (Table 8). Large dissimilarities in populations of *L. rhomboides* ($\rho = 13.03$), *M. beryllina* ($\rho = 4.77$), and *F. similis* ($\rho = 3.4$) were found between occurrences of *C. leucas* versus *N. brevirostris* (Table 8). SIMPER analysis of dissimilarity between occurrences of *C. leucas* versus *R. terraenovae* and *C. limbatus* versus *R. terraenovae* revealed no marked differences in numbers of preferred prey items of either shark species (Table 9 and 10). Fishes most associated with differences in occurrences between *C. leucas* and *R. terraenovae* were *L. rhomboides* ($\rho = 11.8$), *Anchoa mitchilli* ($\rho = 11.1$), *Eucinostomus gula* ($\rho = 3.6$), *M. beryllina* ($\rho = 3.0$), and *Leiostomus xanthurus* ($\rho = 2.8$; Table 9). Fishes most associated with differences in occurrences between *C. limbatus* and *R. terraenovae* were *A. mitchilli* ($\rho = 11.1$), *L. rhomboides* ($\rho = 8.6$), *Eucinostomus gula* ($\rho = 4.8$), *Brevoortia patronus* ($\rho = 3.6$), and *M. beryllina* ($\rho = 3.4$; Table 10). The variables used in the BIO-ENV analysis for changes in fish assemblages at the Chandeleur Islands and Biloxi Marshes were water temperature, secchi depth, salinity, dissolved oxygen, and

the prey preferences of *N. brevirostris, R. terraenovae, C. leucas,* and *C. limbatus*. The percentages of preferred prey items of *N. brevirostris* and *R. terraenovae* had the strongest association with changes in fish assemblages in the Chandeleur Islands and Biloxi marshes (Table 11; BIOENV, $\rho = 0.730$). In connection with the prey preferences of *N. brevirostris* and *R. terraenovae,* salinity was the first environmental variable to have the strongest association with changes in fish assemblages (Table 11; BIOENV, $\rho = 0.724$). Water temperature also appears to play a role with changes in fish assemblages at the Chandeleur Islands and Biloxi marshes (Table 11; BIOENV, $\rho = 0.714$). The BIO-ENV analysis also showed that water turbidity is another environmental variable associated with changes in fish assemblages (Table 11; BIOENV, $\rho = 0.707$). The prey preference for *C. limbatus* was the only other variable to show an association with changes in fish assemblages but this difference was relatively low (Table 11; BIOENV, $\rho = 0.701$).

Table 7: Results of ANOSIM pair-wise comparisons of fish assemblages (i.e., potential prey species) associated with each shark. The groups are divided into different combinations of shark occurrences at the Chandeleur Islands and Biloxi Marshes. The ANOSIM test statistic (R) ranges from 0 to 1 with 1 occurring when all replicate assemblages within a group are more similar to each other than any replicates from different groups. Significant differences ($\alpha < 0.05$) are denoted by an asterisk (*).

Groups	**R**	**p value**
R. terraenovae versus C. leucas	0.52	0.003*
R. terraenovae versus C. limbatus	0.27	0.006*
R. terraenovae versus N. brevirostris	0.01	0.427
R. terraenovae versus R. terraenovae and C. leucas	-0.22	0.915
R. terraenovae versus R. terraenovae and C. limbatus	0.03	0.36
R. terraenovae versus R. terraenovae and N. brevirostris	0.21	0.167
R. terraenovae versus R. terraenovae, C. leucas, and C. limbatus	0.64	0.167
C. leucas versus C. limbatus	0.11	0.079
C. leucas versus N. brevirostris	0.56	0.006*
C. leucas versus R. terraenovae and C. leucas	0.45	0.018
C. leucas versus R. terraenovae and C. limbatus	0.51	0.009*
C. leucas versus R. terraenovae and N. brevirostris	0.53	0.036
C. leucas versus R. terraenovae, C. leucas, and C. limbatus	-0.30	0.7
C. limbatus versus N. brevirostris	0.09	0.225
C. limbatus versus R. terraenovae and C. leucas	0.15	0.177
C. limbatus versus R. terraenovae and C. limbatus	-0.17	0.85
C. limbatus versus R. terraenovae and N. brevirostris	0.22	0.2
C. limbatus versus R. terraenovae, C. leucas, and C. limbatus	-0.18	0.8
N. brevirostris versus R. terraenovae and C. leucas	0.24	0.114
N. brevirostris versus R. terraenovae and C. limbatus	0.72	0.057
N. brevirostris versus R. terraenovae and N. brevirostris	0.36	0.133
N. brevirostris versus R. terraenovae, C. leucas, and C. limbatus	1	0.2
R. terraenovae and C. leucas versus R. terraenovae and C. limbatus	0.82	0.1
R. terraenovae and C. leucas versus R. terraenovae and N. brevirostris	0.42	0.1
R. terraenovae and C. leucas versus R. terraenovae, C. limbatus, and C. limbatus	1	0.25
R. terraenovae and C. limbatus versus R. terraenovae and N. brevirostris	0.5	0.1
R. terraenovae and C limbatus versus R. terraenovae, C. leucas, and C. limbatus	1	0.25
R. terraenovae and N. brevirostris versus R. terraenovae, C. leucas, and C. limbatus	0	0.667

Table 8: Results of SIMPER analysis for the species most associated with differences in fish assemblages between occurrences of *C. leucas* and *N. brevirostris*. The six most dissimilar fish species are shown based on average abundance, average dissimilarity, and cumulative percentage of dissimilarity between occurrences of *C. leucas* and *N. brevirostris*. Prey items found in the diet of YOY and young lemon sharks at the Chandeleur Islands are indicated (*).

Species	***C. leucas* Avg. Abundance**	***N. brevirostris* Avg. Abundance**	**Avg. Diss.**	**Cum. %**
*Lagodon rhomboides**	22.56	492.75	13.03	16.17
Anchoa mitchilli	365.11	0.75	10.17	28.78
*Menidia beryllina**	4.56	71.75	4.77	34.7
Leiostomus xanthurus	9.67	61.5	3.8	39.42
Eucinostomus gula	0	77.75	3.71	44.02
*Fundulus similis**	0.78	36	3.4	48.24

Table 9: Results of SIMPER analysis for the species most associated with differences in fish assemblages between occurrences of *C. leucas* and *R. terraenovae.* The six most dissimilar fish species are shown based on average abundance, average dissimilarity, and cumulative percentage of dissimilarity between occurrences of *C. leucas* and *R. terraenovae*.

Species	***C. leucas* Avg. Abundance**	***R. terraenovae* Avg. Abundance**	**Average Diss.**	**Cum. %**
Lagodon rhomboides	22.56	469.09	11.82	15.31
Anchoa mitchilli	365.11	14.36	11.09	29.68
Eucinostomus gula	0	131.55	3.59	34.33
Menidia beryllina	4.56	59.91	2.97	38.18
Leiostomus xanthurus	9.67	23.82	2.81	41.83
Brevoortia patronus	16.89	0	2.43	44.98

Table 10: Results of SIMPER analysis for the species most associated with differences in fish assemblages between occurrences of *C. limbatus* and *R. terraenovae.* The six most dissimilar fish species are shown based on average abundance, average dissimilarity, and cumulative percentage of dissimilarity between occurrences of *C. limbatus* and *R. terraenovae*.

Species	***C. limbatus* Avg. Abundance**	***R. terraenovae* Avg. Abundance**	**Average Diss.**	**Cum. %**
Anchoa mitchilli	850.67	14.36	11.08	14.82
Lagodon rhomboides	79.67	469.09	8.61	26.35
Eucinostomus gula	107.22	131.55	4.82	32.79
Brevoortia patronus	327.67	0	3.62	37.64
Menidia beryllina	55.11	59.91	3.44	42.24
Harengula jaguana	33.22	18	2.39	45.43

Table 11: Results of BIO-ENV analysis for the changes in fish assemblages at the Chandeleur Islands and Biloxi marshes which indicate the prey preference of *R. terraenovae* and *N. brevirostris* contributed most. A strong correlation between water temperature and salinity also contributed to changes in fish assemblages. The four water quality variables measured were water temperature, secchi depth, salinity, and dissolved oxygen. The prey preference of *N. brevirostris, R. terraenovae, C. leucas, and C. limbatus* was determined by calculating the percent occurrence of the five most preferred prey items in the diet of each shark species.

Number of Variables	Spearman Correlation	Selections
2	0.730	*R. terraenovae* prey preference and *N. brevirostris* prey preference
3	0.724	Salinity, *R. terraenovae* prey preference, and *N. brevirostris* prey preference
4	0.714	Temperature, Salinity, *R. terraenovae* prey preference, and *N. brevirostris* prey preference
4	0.707	Secchi, *R. terraenovae* prey preference, and *N. brevirostris* prey preference
3	0.706	Secchi, Salinity, *R. terraenovae* prey preference, and *N. brevirostris* prey preference
1	0.702	*R. terraenovae prey preference*
5	0.701	Temperature, Salinity, *R. terraenovae* prey preference, *C. limbatus* prey preference and *N. brevirostris* prey preference
6	0.700	Temperature, Secchi, Salinity, *R. terraenovae* prey preference, *C. limbatus* prey preference, and *N. brevirostris* prey preference
5	0.699	Temperature, Secchi, Salinity, *R. terraenovae* prey preference, and *N. brevirostris* prey preference
5	0.699	Secchi, Salinity, *R. terraenovae* prey preference, *C. limbatus* prey preference, and *N. brevirostris* prey preference

Assessing Resource Partitioning between N. brevirostris *and* R. terraenovae

A total of 25 (17 male, 8 female) *R. terraenovae* containing stomach contents were collected from Chandeleur Sound by the GCRL during the summers of 2009 and 2010 (Table 12). Sharks ranged in size from 529 - 965 mm TL. In the study area, juvenile and adult *R. terraenovae* primarily fed on teleost fishes (Table 13). Teleost fishes represented the largest portion of prey items by number (78.6%), frequency of occurrence (84.0%), weight (74.1%), and index of relative importance (88.28%; Table 14). Crustaceans and cephalopods made up the remaining portions of the stomach content. A total of four fish species, two crustaceans, and one cephalopod were identifiable in the stomach contents of adult and sub-adult *R. terraenovae* (Table 10). The identifiable fishes were *Anchoa sp.* (17.9% I_{RI}), *Clupeidae* sp. (0.3% I_{RI}), *Micropogonias undulatus* (1.5% I_{RI}), and *Sciaenops ocellatus* (0.1% I_{RI}; Table 14). The identifiable crustaceans were burrowing sand crabs (*Albuneidae* sp.; 0.2% I_{RI}), penaeid shrimp (*Penaeidae* sp.; 8.4% I_{RI}), and mantis shrimp (*Squilla empusa;* 0.5% I_{RI}; Table 14).

Cumulative prey curves from stomach contents of *R. terraenovae* and *N. brevirostris* were constructed to determine if an adequate number of stomachs had been collected to accurately describe diets. The cumulative prey curve for juvenile *R. terraenovae* does not appear to be approaching an asymptote indicating there were not enough samples examined to describe their diet along with suggesting a more generalized feeding strategy that parallels previous research (Figure 10; Hoffmayer and Parsons, 2003; Parsons and Hoffmayer, 2005). The cumulative prey curves for young *N. brevirostris* do not appear to be approaching an asymptote indicating there were not enough samples examined to describe their diet (Figure 8 and 9). The relatively low sample size in both *N. brevirostris* and *R. terraenovae* resulted in the inability to

Table 12: Biological data on 25 *R. terraenovae* (17 male and 8 female) collected in Chandeleur Sound, Louisiana between 2009 and 2010.

Collection Number	Total weight (g)	TL (mm)	Sex
3SN9 2009	2540	848	Female
5SN1 2009	1000	622	Female
5SN2 2009	920	598	Female
5SN3 2009	1000	627	Female
5SN4 2009	860	609	Female
5SN5 2009	1020	622	Female
5SN57 2009	1580	715	Male
6SN35 2009	2800	859	Male
6SN36 2009	3520	934	Male
6SN37 2009	3720	965	Male
8SN3 2009	350	439	Male
9SN11 2009	3180	864	Male
10SN20 2010	660	529	Female
3SN1 2010	2290	790	Male
5SN45 2010	1660	743	Female
5SN47 2010	1620	738	Male
5SN60 2010	2000	835	Male
5SN61 2010	2950	921	Male
5SN64 2010	3450	930	Male
5SN66 2010	750	600	Male
5SN76 2010	1120	644	Male
5SN78 2010	3160	941	Male
7SN12 2010	2500	859	Male
7SN13 2010	2780	876	Male
7SN14 2010	2100	822	Male

Table 13: Stomach contents of 25 *R. terraenovae* (17 male and 8 female) collected from 2009 to 2010 survey of Chandeleur Sound by the Gulf Coast Research Laboratory of the University of Southern Mississippi

Collection Number	Contents	Quantity	Weight (g)
3SN9 2009 (female)	Unknown teleost remains	1	5.9
5SN1 2009 (female)	*Anchoa mitchilli*	4	12.4
5SN2 2009 (female)	*Penaeus aztecus*	1	4.2
5SN3 2009 (female)	*Anchoa mitchilli*	12	27.3
	Unknown teleost remains	1	9.12
	Penaeidae sp.	1	1.05
5SN4 2009 (female)	*Anchoa mitchilli*	1	3.1
5SN5 2009 (female)	*Penaeus duorarum*	1	13.6
5SN57 2009 (male)	*Penaeus aztecus*	1	3.41
6SN35 2009 (male)	*M. undulatus otolith*	1	0.06
	Unknown teleost remains	1	0.14
6SN36 2009 (male)	*Squilla empusa*	1	2.78
	M. undulatus otoliths	2	0.113
	Penaeidae sp.	1	0.31
6SN37 2009 (male)	*Penaeidae* sp.	1	1.38
	Unknown teleost remains	1	1.03
8SN3 2009 (male)	*Micropogonias undulatus*	1	3.38
9SN11 2009 (male)	*Micropogonias undulatus*	1	2.3
10SN20 2010 (female)	*Sciaenops ocellatus*	1	1
3SN1 2010 (male)	*Anchoa* sp.	1	2.7
5SN45 2010 (female)	Unknown teleost remains	1	0.5
5SN47 2010 (male)	Unknown teleost remains	1	0.3
5SN60 2010 (male)	*Anchoa mitchilli*	2	4.2
	Penaeidae sp.	1	2.3
	Squilla empusa	1	4.1
5SN61 2010 (male)	*Anchoa mitchilli*	6	3.8
	Unknown teleost remains		1.3
5SN64 2010 (male)	*Penaeidae* sp.	1	2.8
5SN66 2010 (male)	*Anchoa* sp.	1	0.8
5SN76 2010 (male)	*Clupeidae* sp.	1	8.8
5SN78 2010 (male)	*Albuneidae* sp.	2	2.3
7SN12 2010 (male)	Unknown teleost remains	1	0.1
7SN13 2010 (male)	Unknown teleost remains	1	1.4
7SN14 2010 (male)	Unknown teleost remains	1	0.2

Table 14: Diet composition of *Rhizoprionodon terraenovae* collected in Chandeleur Sound, Louisiana from 2009 to 2010 (n=25)

Food item	**N**	**%**	**F**	**%**	**wt (g)**	**%**	**I_{RI}**	**%I_{RI}**
Teleost	44	78.6%	21	84.0%	89.8	74.1%	1.28	88.3%
Anchoa sp.	27	48.2%	7	28.0%	54.3	44.8%	0.26	17.9%
Clupeidae sp.	1	1.8%	1	4.0%	8.8	7.3%	0.00	0.3%
M. undulatus	5	8.9%	4	16.0%	5.7	4.7%	0.02	1.5%
Sciaenops ocellatus	1	1.8%	1	4.0%	1.0	0.8%	0.00	0.1%
Unid teleosts	10	17.9%	10	40.0%	20.0	16.5%	0.14	9.5%
Crustacean	12	21.4%	9	36.0%	31.4	25.9%	0.17	11.7%
Albuneidae sp.	2	3.6%	1	4.0%	2.3	1.9%	0.00	0.2%
Penaeidae	8	14.3%	8	32.0%	29.1	24.0%	0.12	8.4%
Squilla empusa	2	3.6%	2	8.0%	6.9	5.7%	0.01	0.5%

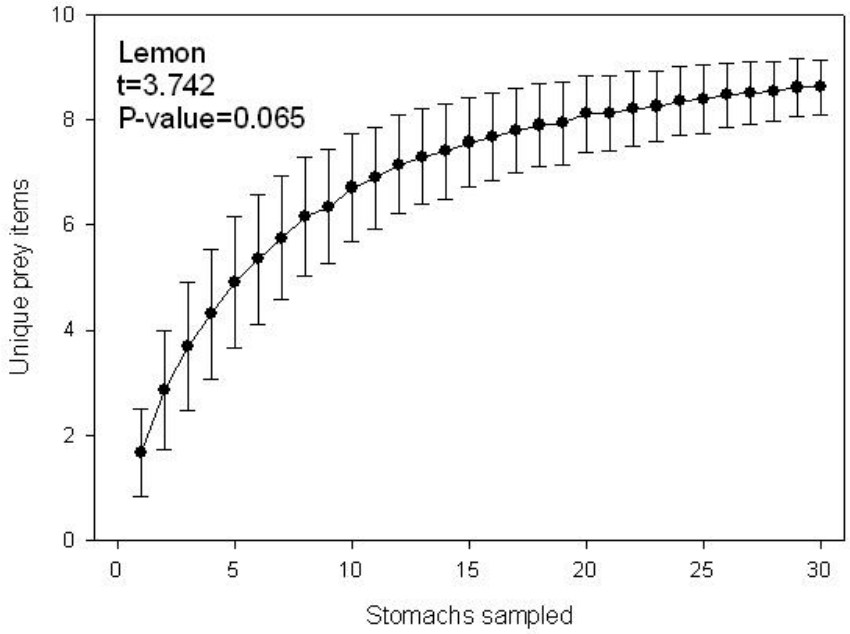

Figure 8: Cumulative prey curve for young *N. brevirostris* collected at the Chandeleur Island nursery habitat (n=30). Identifiable and unidentifiable stomach contents are included.

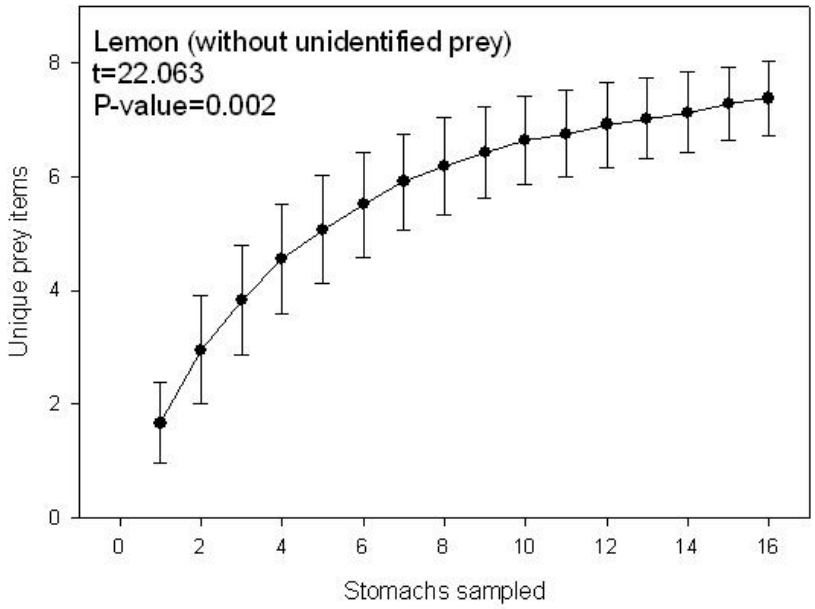

Figure 9: Cumulative prey curve for young *N. brevirostris* collected at the Chandeleur Island nursery habitat (n=16). Only those sharks containing identifiable stomach contents are included.

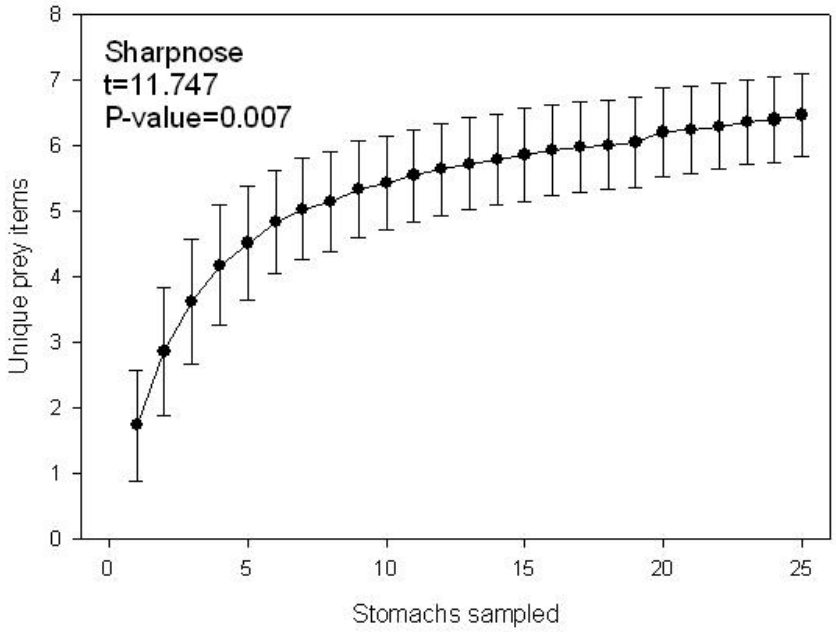

Figure 10: Cumulative prey curve for juvenile *R. terraenovae* collected in Chandeleur Sound (n=25)

accurately describe their diets. The diet of juvenile and adult *N. brevirostris* at the Chandeleur Islands also needs to be examined to determine whether sharks have any dietary overlap between life-stages or do sharks exhibit an ontogenetic shift in their diet like those in Bimini, Bahamas.

Discussion

Diet and Prey Availability of Young N. brevirostris *at the Chandeleur Islands*

Young *N. brevirostris* at the Chandeleur Island nursery habitat have a more limited diet breadth than those found in Bimini, Bahamas and the Florida Keys. Young *N. brevirostris* from the Florida Keys and Bimini, Bahamas fed on more than 25 different families of teleosts, elasmobranchs, mollusks, and crustaceans (Cortés and Gruber, 1990) while those at the Chandeleur Islands fed on less than 10 different families of teleosts and crustaceans. The diet of juvenile *N. brevirostris* in the North Sound and South Bimini, Bahamas was composed of 31 different families of teleosts, elasmobranchs, crustaceans, mollusks, and annelids (Newman et al., 2010). Young *N. brevirostris* at the Chandeleur Island nursery habitat are feeding on similar prey items to those at the Florida Keys and Bimini, Bahamas including silversides (Atherinidae), killifishes (Cyprinodontidae), and porgies (Sparidae), swimming crabs (Portunidae), and penaeid shrimps (Penaeidae; Cortés and Gruber, 1990; Newman et al., 2010). Young *N. brevirostris* at the Bimini nursery habitat fed on small fishes that school over shallow grass beds such as killifishes and silversides (Cortés and Gruber, 1990). Nocturnal feeding activity in *N. brevirostris* has also been suggested with increases in activity and metabolic rate in sharks with the onset of darkness in laboratory settings (Gruber 1984). The diet of young *N. brevirostris* at the Chandeleur Islands appears to be limited to the most abundant prey items available at the

Chandeleur Islands. Previous studies have also shown juvenile *N. brevirostris* to feed on the most abundant organisms in the shallow water environments inhabited by the sharks (Wetherbee et al., 1990). The three primary prey items that compose the diet of young *N. brevirostris* at the Chandeleur Islands were *L. rhomboides, M. beryllina,* and *F. similis*. In regard to availability in the same area, these prey species rank number one, three, and ten respectively, suggesting that *N. brevirostris* at the Chandeleur Islands are also feeding on the most abundant prey species available.

The primary prey items for young *N. brevirostris* are most commonly found in seagrasses throughout the Chandeleur Islands. Seagrass beds are among the most productive aquatic ecosystems and may increase biodiversity of associated organisms utilizing this habitat as a nursery, foraging area, or predation refuge (Gullström et al., 2002). Young *N. brevirostris* were most commonly found cruising in the shallow water sand flats during the day avoiding predation from larger predatory sharks that are unable to access these habitats (personal observation). Juvenile *N. brevirostris* confine their activities to water depths that are too shallow to be entered by their predators (Morrissey and Gruber, 1993). Seagrass habitats that were accessible to larger sharks during the day were avoided by smaller *N. brevirostris* until dusk (personal observation). At the Chandeleur Islands, tidal cycles reduce the depth of seagrass habitats at night preventing larger sharks from accessing these areas and allowing young *N. brevirostris* the opportunity to feed on small schooling fishes. For example, on 11 May 2009 at 2015 one small *N. brevirostris* was caught in the seagrass beds and found to contain nine *M. beryllina,* one *L. rhomboides,* one *F. similis* and one *S. foetens.* All stomach contents had been recently digested. The movement patterns of *C. leucas* within nursery habitats have also been correlated with tidal stage and the distribution and movement patterns of their prey species (Ortega et al., 2009). The use of

currents for movements to and from muddy littoral zones that contained an abundance of food has been shown to potentially conserve 6% of the total energy expenditure in the leopard shark (*Triakis semifasciata;* Ackerman et al., 2000). Neonate *C. limbatus* were also observed aggregating during the day as a means of predator avoidance, then dispersing at night indicating a shift into a feeding mode (Barry et al., 2008). Neonate and juvenile *C. limbatus* in the Timbalier-Terrebonne Bay complex began feeding as darkness increased and continued feeding until daylight returned (Barry et al., 2008). It appears that most sharks, including *N. brevirostris*, rely on the use of tidal currents for foraging and predator avoidance within nursery habitats.

The limited diet breadth of young *N. brevirostris* at the Chandeleur Island nursery habitat may signify a preference according to prey species and prey size. Juvenile *N. brevirostris* in the North Sound, Bimini had a strong preference for the most abundant and diverse prey communities feeding opportunistically on Gerreidae spp. because they were abundant in the environment (Newman et al., 2010). Sharks off South Bimini continued to consume large numbers of Gerreidae spp. despite their lower abundance in the environment, revealing the true high degree of preference for Gerreidae spp. by juvenile *N. brevirostris* (Newman et al., 2010). Young *N. brevirostris* at the Chandeleur Islands nursery habitat seem to fit the profile of feeding opportunistically on the most abundant prey items in the environment. For example, I commonly observed young *N. brevirostris* in areas with the highest abundance of preferred prey items during foraging activities. Habitat selection based primarily on prey availability has been shown to occur throughout marine environments. Individual crown urchins (*Centrostephanus coronatus*) that occur where their most preferred food is common, consume primarily that one food type, whereas urchins that occur where it is rare add other foods to their diets (Vance and Schmitt, 1979). Overgrazing by individual urchins of their most preferred food has resulted in

the inclusion of less preferred foods in the diet (Vance and Schmitt, 1979). Population structure and composition can be influenced by selective foraging resulting in shifts to less preferred prey items, as observed with juvenile *N. brevirostris* off south Bimini (Newman et al., 2010). If the limited diet breadth of young *N. brevirostris* at the Chandeleur Islands is a result of showing preference for *L. rhomboides, M. beryllina,* and *F. similis,* then those sharks may perhaps be shaping population structure and composition of fish assemblages through selective foraging. However, recent increases in the population of *F. similis* may be caused by a post-Hurricane Katrina increase in habitat edge effects (Ellinwood, 2008). As tropical cyclones and sea level rise increase habitat edge (and potential prey fishes that use these edge habitats), a possible result is that *N. brevirostris* may begin to rely more on these species in their diet. The limited diet breadth of young *N. brevirostris* at the Chandeleur Islands appears to be an opportunistic feeding strategy that exploits the most abundant prey items. The increase in edge habitat species in the diet of young *N. brevirostris* demonstrates the shark's plasticity to opportunistically feed based on the local environmental conditions.

Land loss and landward migration of the Chandeleur Islands will result in unsuitable conditions as a pupping ground for *N. brevirostris* in the future. The gulf and bay shorelines are rapidly migrating landward, but the gulf shoreline is migrating twice as fast, resulting in the island narrowing by 50% (McBride and Byrnes, 1997). I observed a majority of young *N. brevirostris* occurring in areas with the greatest landmass and habitat diversity. Chandeleur Island site C-2 contains the healthiest marsh habitat portion of the island and contained the greatest abundance of young *N. brevirostris* in and around the area. Current research has projected the Chandeleur Islands to maintain itself, especially the robust north-central portion, however the southern end appears vulnerable to island breaching and the backbarrier islands will

most likely disappear in the near future (McBride and Byrnes, 1997). The southern Chandeleur Islands (Curlew and Grand Gosier Islands) are ephemeral barrier islands undergoing early stages of transgressive submergence and conversion into an inner shelf shoal (Fearnley et al., 2009). These islands have been destroyed and converted into submerged shoals due to periods of high storm frequency and intensity (Fearnley et al., 2009). The northern Chandeleur Islands are now experiencing similar erosional impacts due to frequent intense storms, and are expected to be completely converted into ephemeral barrier island/shoals between 2013 and 2037 (Fearnley et al., 2009). The Chandeleur Islands serve as a valuable nursery habitat because young *N. brevirostris* are able to exploit and utilize the habitat heterogeneity throughout the island chain. The Chandeleur Islands contain multiple habitat types including rich, productive seagrass beds, wide shallow sand flats, and marsh fringe habitat containing black mangroves. The rapid decline and loss of these habitat types in the far northern and southern portion of the Chandeleur Islands will reduce the viable areas as nursery habitats and reduction in home range of young *N. brevirostris*. Home ranges of most young sharks are narrow expanses close to shore (Morrissey and Gruber, 1993). Young, inexperienced *N. brevirostris* have shown an innate ability to home suggesting high site fidelity to their original home range (Clermont and Gruber, 2005). Sharks that are strongly philopatric to a specific habitat are at a significant disadvantage due to the impacts of habitat loss and decreased production (Carlson et al., 2008). Shark species that are highly dependent on specific habitat and use restricted portions of nearshore areas are probably the most vulnerable when environmental conditions extend beyond their physical limitations (Knip et al., 2010). The Chandeleur barrier system has no outside sediment source and is located on a subsiding deltaic surface, resulting in the current narrowing and lowering in profile of the island chain (Kahn, 1986). In addition to seasonal and regular changes, the Chandeleur Islands

are highly susceptible to sudden events such as storms and weather phenomena that can affect the structure and characteristics of this habitat. The continued loss of land area and habitat structure throughout the islands will result in the creation of broad areas of open water that will no longer serve as protective, shallow water habitats for young *N. brevirostris*.

Distribution and Prey Selectivity of Four Shark Species

The distributions of *N. brevirostris, R. terraenovae, C. leucas,* and *C. limbatus* vary in southeastern Louisiana. The distribution of *N. brevirostris* was the smallest of all four shark species with occurrences only at the Chandeleur Island sites. The inability to tolerate small changes in salinity limits the distribution of *N. brevirostris* to only the barrier island system (Morrissey and Gruber, 1993). The highest abundance of *N. brevirostris* was observed at the north-central Chandeleur Island site C-2. The distribution of *R. terraenovae* was more widespread with occurrences at all four Chandeleur Island sites and site B-2 at Grand Pass. Despite being one of the smallest coastal shark species, *R. terraenovae* do not use a discrete habitat but likely utilize a series of coastal bays and estuaries throughout the juvenile stage (Carlson et al., 2008). The distribution of *C. leucas* was the largest of the four shark species with similar abundances observed at all seven sites between the Chandeleur Islands and Biloxi Marshes. The ability of *C. leucas* to physiologically tolerate a wide-range of salinities allows them to maximize their use of coastal bays, estuaries, and riverine environments (Simpfendorfer et al., 2005; Parsons and Hoffmayer, 2007; Ortega et al., 2009). The distribution of *C. limbatus* was similar to that of *R. terraenovae* with occurrences at all four Chandeleur Island sites as well site B-2 at Grand Pass and B-1 at Half Moon Island. Research has shown that *C. limbatus* are

common inhabitants of inshore coastal and estuarine regions throughout the Gulf of Mexico (Killam and Parsons, 1989), but recent captures of blacktip sharks in salinities as low as 11 PSU, has suggested that this species may be more euryhaline than was previously recognized (Parsons and Hoffmayer, 2007). Clearly, of these species, *N. brevirostris* exhibits the most restricted distribution and this may have conservation consequences in the near future.

The distribution of different shark species can be influenced by predation pressure from one species on another. I found differences in fish assemblages among occurrences of *R. terraenovae* and *C. leucas, R. terraenovae* and *C. limbatus*, and *N. brevirostris* and *C. leucas* and predation pressure may play a role in these differences. Small YOY are highly susceptible to predation by larger sharks if they occur in similar habitats. For example, the presence of sandbar sharks (*C. plumbeus*) in the diet of tiger sharks (*Galeorcerdo cuvier*) and the inverse relationship in catch per unit effort of these two species in Hawaii indicates that *G. cuvier* predation on *C. plumbeus* may influence their distribution (Papastamatiou et al., 2006). The main predators of young *R. terraenovae* at the Chandeleur Islands and Biloxi Marshes are larger *C. leucas* and *C. limbatus* (personal observation). The difference in fish assemblages between these three species possibly reflects *R. terraenovae* avoiding those habitats where its natural predators are likely to occur. Nearby along the Mississippi and Alabama gulf coasts, large juvenile *C. limbatus* and *C. isodon* are considered predators of small YOY *R. terraenovae* (Parsons and Hoffmayer, 2007). Episodes of predation on free-swimming YOY *R. terraenovae* by larger, unidentified shark species have been documented (Parsons and Hoffmayer, 2007). The same situation applies towards larger *C. leucas* which are the natural predators for young *N. brevirostris* at the Chandeleur Islands nursery habitats. Multiple times young *N. brevirostris* were observed with teeth marks and wounds due to predation from larger sharks (Figure 9). The cannibalistic

tendencies of both *N. brevirostris* and *C. leucas* are well documented (Vorenberg, 1962; Snelson et al., 1984). Shark tissue has also been regularly identified as a prey item in the stomach content of various shark species (Snelson et al., 1984; Hoffmayer and Parsons, 2003; Parsons and Hoffmayer, 2007). With all of this predation pressure associated with the presence of other sharks, the ability of small sharks to find shallow water coastal areas that are low in predation pressure significantly increases the likelihood of surviving into adulthood.

The factors that were found to be most associated with differences in fish assemblages and shark occurrences were the preferred prey items of *R. terraenovae* and *N. brevirostris*. More simply, young *R. terraenovae* and *N. brevirostris* appear to be selectively tracking prey items in low predation environments, more so than either *C. leucas* or *C. limbatus*. Because small *R. terraenovae* and *N. brevirostris* are vulnerable to predation by larger sharks (see above), they are thus forced to select shallow water habitats with abundant food resources. These shallow habitats will also have decreased competition because larger sharks cannot occur there. Dissimilarity matrices showed significant differences in the numbers of *L. rhomboides, M. beryllina,* and *F. similis* (the preferred prey items of YOY *N. brevirostris* at the Chandeleur Island nursery habitat) between occurrences of *N. brevirostris* and *C. leucas.* Young *N. brevirostris* are keying in on habitats that are high in prey availability and low in predation pressure. Ecological factors such as prey availability, predation risk, and the presence of competitors determine selection of appropriate habitat (Sims, 2003). Competition and predation are both fundamental components of the environment that influence community structure (Papastamatiou et al., 2006). For example, the habitat use of small bluegill (*Lepomis macrochirus*) suggests that these fish balance foraging profitability and predation risk when selecting habitats, and that this balance is a dynamic one depending on prey availabilities and

Figure 11: Young *N. brevirostris* with large teeth wounds along the ventral surface collected at the Chandeleur Islands, Louisiana. Young *N. brevirostris* can be prey items for larger, predatory sharks.

relative risks (Mittelbach, 1981). Juvenile *N. brevirostris* in Bimini, Bahamas generally select the shallow water, thick mangrove-fringe shorelines due to the high food abundance and complex habitat as a means of avoiding predators by decreasing encounter and predation rate (Morrissey and Gruber, 1993). Juvenile sharks in Cleveland Bay, Australia generally selected the highly productive mangrove and seagrass habitats because it supports large populations of preferred prey items and reduced predation from adult sharks (Simpfendorfer and Milward, 1993). Young *N. brevirostris* and *R. terraenovae* appear to be selecting prey items that have little dietary overlap with other species. The combination of a high diversity of prey types and a high percentage of multiple prey types within their diet suggests that *R. terraenovae* is a generalist feeder (Hoffmayer and Parsons, 2003). Observed diet overlap in Apalachicola Bay was very low between YOY *R. terraenovae* and all life-stages of *C. isodon* and *C. brevipinna* (Bethea et al., 2004). The appearance of pelagic teleosts and benthic crustaceans in the diet of small *N. brevirostris* and *R. terraenovae* further demonstrates their feeding plasticity (Newman et al., 2010). Although habitats occupied by juvenile *R. terraenovae* in Florida are not food limited, sharks may be frequenting multiple areas in search of higher quality food to support their high levels of growth during early life stages (Carlson et al., 2008). Feeding opportunistically in low predation environments at the Chandeleur Islands by *N. brevirostris* and *R. terraenovae* likely helps to reduce competition for food resources while maximizing growth and survivorship for both species. The fact that both species appear to be closely tracking these specific prey items further emphasizes possible conservation issues in the future for *N. brevirostris* and *R. terraenovae*, at least relative to the larger *C. leucas* and *C. limbatus*.

Temperature and salinity were secondary factors associated with differences in fish assemblages and shark occurrences. Water temperature is a central factor controlling the rate of

physiological processes, including growth patterns in sharks (Sims, 2003). Unlike mammals, shark body temperatures are dependent on the external environment (Sims, 2003), making habitat choice an important physiological decision. Temperature can have an immediate impact on shark distributions and activity patterns particularly during summer months when water temperature is high and the potential for low dissolved oxygen exists (Parsons and Hoffmayer, 2005). Although temperature at the Chandeleur Islands and Biloxi Marshes fluctuated between 19-31° C from March to November, dissolved oxygen levels remained high indicating sufficient water exchange. Collections of *N. brevirostris* occurred in the highest temperature range with occurrences between 27.2 and 32.0° C. Juvenile *N. brevirostris* have been shown to primarily select water temperature greater than 30° C due to their hematological characteristics that enable them to respire in warm water (Morrissey and Gruber, 1993). The ability to not only adapt but select the warm water sand flats allow young *N. brevirostris* to maintain optimal metabolic performance (Morrissey and Gruber, 1993). This ability may also help explain why young *N. brevirostris* dominate the shallow water habitats at the Chandeleur Islands during summer months. Should the islands erode further and become a shoal in the near future, these shallow habitats will no longer exist and be able to offer protection to this species. The temperature range for collections of *R. terraenovae* and *C. leucas* were similar with sharks occurring between 19 and 32° C. Thermal and hypoxic stress in adult male *R. terraenovae* has been shown with increases in temperature approaching or exceeding 30° C indicating that temperature plays a role in where this species occurs (Parsons and Hoffmayer, 2005). Temperature has also been shown to play a role in the distribution and movement patterns of juvenile *C. leucas* within estuaries (Heupel and Simpfendorfer, 2008; Ortega et al., 2009). I found the temperature range for *C. limbatus* in southeastern Louisiana was 21.2 to 32.0° C. Increases in catches of YOY and

neonate *C. limbatus* have been positively correlated with increased temperature in July and August in the north-central Gulf of Mexico (Parsons and Hoffmayer, 2007). Interestingly, no sharks were caught in waters greater than 32.0° C indicating a possible limit for higher temperatures in all four shark species.

Salinity was also an environmental variable that was associated with differences in fish assemblages and shark occurrences at the Chandeleur Islands and Biloxi Marshes. In euryhaline species, the energetic cost of osmoregulation varies with salinity, suggesting that the use of salinity-selection behavior is related to energy allocation (Heupel and Simpfendorfer, 2008). The role of salinity as a determining factor in the distribution and movement patterns of few shark species has recently been investigated. This research has determined that the utilization of a wide-range of salinity levels by bonnethead sharks (*Sphyrna tiburo*) allows them to use a large portion of the available habitat within an estuary (Ubeda et al., 2009). The salinity range for collections of *N. brevirostris* and *R. terraenovae* were similar with sharks occurring between 19 and 32 PSU. Juvenile *N. brevirostris* in Bimini used regions of differing salinity in proportion to availability and these regions did not seem to be important in terms of habitat selection (Morrissey and Gruber, 1993). Strong relationships between the effects of salinity and captures of *R. terraenovae* have been observed along the Mississippi and Alabama gulf coasts with sharks captured at significantly higher salinities than *C. limbatus* and *C. isodon* suggesting that *R. terraenovae* may be less euryhaline than originally thought (Parsons and Hoffmayer, 2007). The salinity range for collections of *C. leucas* was the widest of all four species with sharks occurring between 2.2 and 27.5 PSU. These results are not surprising considering the physiological capability to tolerate fresh, estuarine, and marine waters for extended periods of time (Simpfendorfer et al., 2005; Parsons and Hoffmayer, 2007; Ortega et al., 2009). Previous

research has determined that salinity is an important factor in determining the distribution and occurrences of differing age classes of *C. leucas* (Simpfendorfer et al., 2005). Recent research on *C. leucas* has suggested that their use of freshwater systems is not based on physiology, but rather a strategy to take advantage of increased prey resources and decreased competition (Heupel and Simpfendorfer, 2008). In any case, the occurrence of *C. leucas* in waters less than 10 PSU provides sharks with greater habitat and food availability opportunities. The salinity range for collections of *C. limbatus* was the most surprising of all four species with sharks occurring between 4.3 and 31.6 PSU. Captures of *C. limbatus* in extremely low saline waters are rare but suggest that this species may be more euryhaline than was previously recognized. The captures of *C. limbatus* in salinities as low as 11 PSU have only recently been discovered, but the occurrences of sharks in salinities of only 4 PSU in the current study appear to be unprecedented.

Nearshore environments like the Chandeleur Islands and Biloxi Marshes typically consist of shallow water with temporally varying characteristics and are commonly comprised of highly dynamic ecosystems supporting high biodiversity (Knip et al., 2010). Although variable conditions such as major fluctuations in salinity, temperature, depth, flow, and turbidity due to changes in tidal level, freshwater flow, rainfall, and seasonal weather patterns create challenging environments for inhabitants, nearshore environments are highly productive (Knip et al., 2010). Sharks are a key component of nearshore ecosystems that utilize these areas in different ways by different species. The characteristics and habitat types in a region may, therefore, influence the distribution and movement of local shark species (Knip et al., 2010). Thus, habitat use by sharks within nearshore environments is likely to be influenced by a combination of ecological factors including environmental characteristics, resource abundance, predation pressure, or competition with other shark species (Sims, 2003; Knip et al., 2010). The significant differences in shark

occurrences between *R. terraenovae* and *C. leucas* and *C. limbatus* along with differences between *N. brevirostris* and *C. leucas* likely indicate differences in habitat selection as a means for predator avoidance. For example, smaller *N. brevirostris* and *R. terraenovae* are more closely associated with each other than larger sharks like *C. leucas* and *C. limbatus*. The occurrence of juvenile *C. limbatus* at the Chandeleur Islands and Biloxi Marshes indicates this species can transition between those habitats associated with smaller *R. terraenovae* and *N. brevirostris* and those habitats associated with larger *C. leucas*.

The changes in distribution and habitat selection by the four shark species at the Chandeleur Islands and Biloxi Marshes is influenced by a combination of abiotic factors such as temperature and salinity, but also ecological factors such as prey availability, predation risk, and the presence of competitors. My data suggest that temperature and salinity play large roles in the distribution of all four species, with the physiological capabilities of each species appearing to be key determinants. The prey preference of *N. brevirostris* and *R. terraenovae* were the factors most associated with changes in fish assemblages and shark occurrences. Young *N. brevirostris* and *R. terraenovae* generally occur in shallow water habitats that are low in predation but high in food abundance which allows them to be opportunistic feeders on the most abundant prey items. The confinement to shallow water habitats in order to avoid predation may describe the lowered diet breadth in young *N. brevirostris* at the Chandeleur Islands. Predator avoidance by small *N. brevirostris* and *R. terraenovae* may result in the selection of shallow water habitats that are high in prey abundance but low in prey diversity.

Assessing Resource Partitioning between N. brevirostris *and* R. terraenovae

There is no dietary overlap between *N. brevirostris* and *R. terraenovae* in Chandeleur Sound. Although, *R. terraenovae* were collected in Chandeleur Sound and *N. brevirostris* were captured in the shallow water habitats of the Chandeleur Islands, both shark species were of similar size ranges. Collections of *R. terraenovae* containing stomach contents ranged from 529-965 mm TL while *N. brevirostris* containing stomach contents ranged from 628-1430 mm TL. Collections of *R. terraenovae* in Chandeleur Sounds by the Gulf Coast Research Laboratory were juveniles while *N. brevirostris* captured at the Chandeleur Island nursery habitat were primarily YOY. In the north-central Gulf of Mexico, *R. terraenovae* are among the smallest of coastal shark species as juveniles (Carlson et al., 2008) and are similar in size to young *N. brevirostris* born that year. Despite their small size, *R. terraenovae* do not use discrete shallow water habitats but a series of coastal bays and estuaries throughout the juvenile stage forming a homogenous habitat for juvenile production (Carlson et al., 2008). Although *R. terraenovae* have high levels of natural mortality they are among those sharks with the highest productivities with estimates of intrinsic rates of increase of approximately 16% per year (Carlson et al., 2008). The ability to frequent multiple areas in search of higher quality food to support their high levels of growth during early stages (Carlson et al., 2008), being an opportunistic and generalized predator (Hoffmayer and Parsons, 2003; Parsons and Hoffmayer, 2005), and undergoing a significant ontogenetic dietary shift (Hoffmayer and Parsons, 2003; Bethea et al., 2006) reducing competition for resources enable *R. terraenovae* to be the most ubiquitous coastal shark in the Gulf of Mexico.

The diet of *R. terraenovae* collected in Chandeleur Sound contained primarily estuarine pelagic teleosts including *A. mitchilli, M. undulatus* and penaeid shrimp. Teleost fishes have been shown to the dominant food category in the diet of all life-stages of *R. terraenovae*

(Hoffmayer and Parsons, 2003; Bethea et al., 2004; Bethea et al., 2006). The diet of *R. terraenovae* has been show to vary depending on where they were collected (Bethea et al., 2006). The diet of young of the year *R. terraenovae* collected in Mississippi Sound consisted of teleost prey including *A. mitchilli* and *B. patronus*, penaeid shrimp, and squid while juveniles consisted primarily of teleosts including *B. patronus* and penaeid shrimp (Hoffmayer and Parsons, 2003). The diet of YOY *R. terraenovae* collected in Apalachicola Bay consisted of primarily of penaeid shrimp with *M. undulatus* the second most important prey item while juveniles primarily consisted of Cynoscion sp. but also included penaeid shrimp and gafftop sail catfish (*Bagre marinus*; Bethea et al., 2004). In Crooked Island Sound, Florida clupeids were important in the diet of all three life-stages of *R. terraenovae* with penaeid shrimp and several different species of sciaenids composing the remaining portions (Bethea et al., 2006). In contrast, penaeid shrimp were important in the diet of all three life-stages at St. Vincent Island with *M. undulatus, C. nothus,* and *B. patronus* composing the remaining portions (Bethea et al., 2006). Geographic differences in the diet are most likely due to associations between life-stage, habitat, and prey availability (Bethea et al., 2006).

The differences in habitat selection between similar sized *R. terraenovae* and *N. brevirostris* result in no dietary overlap between these two shark species. The cumulative prey curves for young *N. brevirostris* did not reach an asymptote indicating there were not enough stomachs examined to accurately describe their diet within the Chandeleur Island nursery habitat. The cumulative prey curve for *R. terraenovae* also did not reach an asymptote indicating there were not enough stomachs analyzed to accurately describe their diet. The increased number of prey items within the diet of *R. terraenovae* suggests a more generalized feeding strategy by sharks in Chandeleur Sound. Sample size needs to be increased in both species in order to

accurately describe their diets. Observations of YOY *R. terraenovae* in the shallow water habitats of the Chandeleur Islands have shown the utilization of this area by *R. terraenovae* indicating possible habitat overlap with YOY *N. brevirostris*. The diet of YOY *R. terraenovae* at the Chandeleur Islands needs to be examined to determine differences in diet from other nursery habitats and determine any dietary overlap with YOY *N. brevirostris*. The diet of juvenile and adult *N. brevirostris* at the Chandeleur Islands also needs to be examined to determine whether sharks have any dietary overlap between life-stages or do sharks exhibit an ontogenetic shift in their diet like those in Bimini, Bahamas.

Conclusions

The Chandeleur Islands, Louisiana serve as an important nursery habitat for *N. brevirostris* by offering high abundances of prey items and increased protection from predators resulting in increased recruitment into the adult population. Young *N. brevirostris* at the Chandeleur Island nursery habitat have a limited diet breadth compared to those found in nurseries in Bimini, Bahamas and the Florida Keys. Young *N. brevirostris* appear to be opportunistically feeding on the most abundant prey items at the Chandeleur Islands resulting in high prey abundance and low diversity in their diet. Opportunistic feeding by young *N. brevirostris* suggests minimal dietary overlap with other shark species occurring at the Chandeleur Islands resulting in minimal competition for resources. Habitat selection at the Chandeleur Islands and Biloxi Marshes by *N. brevirostris* and *R. terraenovae* appears to be driven by predation from larger sharks and high prey availability together. Significant differences in fish assemblages and shark occurrences were observed between *R. terraenovae* and *C. leucas* and *C. limbatus* as well as differences between *N. brevirostris* and *C. leucas.*

Abiotic and ecological factors such as temperature, salinity, prey preference of *N. brevirostris* and *R. terraenovae*, and predator avoidance are most associated with differences in shark occurrences at the Chandeleur Islands and Biloxi Marshes.

Further research into the biology and ecology of all sharks is needed because little is still known about these apex predators. For example, the presence of *C. limbatus* occurring in extreme euryhaline conditions has only recently been discovered and publicized. The recent discovery of the Chandeleur Islands as a nursery habitat by the Nekton Research Lab has tremendous implications on whether this barrier island system will continue to serve as a nursery for *N. brevirostris*. The Chandeleur Islands are continuing to experience rapid land loss, landward migration, habitat degradation, and sudden catastrophic events such as tropical cyclones which may result in the displacement of young *N. brevirostris*. Displacement from a species' original or preferred habitat to other regions may have consequences such as reduced habitat quality, decreased food availability, increased predation risk, or increased competition with other species. Research has only begun to determine the role of barrier islands on various life-stages in sharks and the consequences to relying on unpredictable nearshore areas. The development of Fisheries Ecosystem Plans, management plans that require the consideration of all biotic, abiotic, and human related-interactions with the target stock as well the designation of Essential Fish Habitats need to be further researched in marine coastal environments. Continuing advances in research and management of sharks in the future will help to discover how important these apex predators are to the world's aquatic ecosystems.

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Appendix I – IACUC Approval

Institutional Animal Care and Use Committee

UNIVERSITY OF NEW ORLEANS

DATE: August 13, 2009

TO: Dr. Martin T. O'Connell

FROM: Steven G. Johnson, Ph.D.
Chairman

RE: *IACUC Protocol* # **UNO-09-009**
Entitled: Establishing a unified tagging program to assess post-hurricane fisheries in the Pontchartrain Basin

Your application for the use of animals in research (referenced above) has been approved beginning August 13, 2009 and expiring August 12, 2011. Please note that an annual/final report must be provided to the UNO IACUC.

The University of New Orleans has an Animal Welfare Assurance on file with the Office of Laboratory Animal Welfare (OLAW), National Institutes of Health. The assurance number is A3299-01.

Vita

Christopher Dennis Davis was born November 18, 1984 in New Haven, Connecticut. His parents Brian and Renee Davis raised him and his brother Thomas in West Haven and East Haven, Connecticut for much of their lives. Christopher was also enthusiastic about sports and the outdoors. Growing up he loved sharks and always wanted study them which earned him the nickname shark-bait from his mother. Christopher had always put an importance on education, challenging himself on the highest level, and always working hard and beyond his potential which was instilled in him by his parents. He received his Bachelors of Science Degree in Marine Biology from Roger Williams University in Bristol, Rhode Island where he became interested in fisheries. After entering the job force and finding no chances to work in the marine biology field Christopher finally received the opportunity he had been waiting for to work with sharks at the University of New Orleans. Christopher wants to continue working in fisheries wherever it might take him.